ABSTRACT

Title of dissertation: **HUNTER-GATHERERS, ARCHAEOGENOMICS, AND THE EVOLUTIONARY HISTORY OF THE FOXES OF CALIFORNIA'S CHANNEL ISLANDS**

Courtney A. Hofman, Doctor of Philosophy, 2015

Dissertation directed by: Professor Paul Shackel, Department of Anthropology

Understanding human-animal relationships is a fundamental area of archaeological research. Throughout human history, animals have been sources of food, raw materials, labor, and companionship. Humans have also had an important influence on animal populations, including extinction, domestication, and translocation. Recently, archaeological research on the interactions between humans and animals has also helped us understand the contemporary status of animal populations, providing important insights for conservation biology and establishing a new research agenda, conservation archaeogenomics. In this dissertation, I define the field of conservation of archaeogenomics and develop a case study of how archaeological, genomic, and isotope data can be integrated to inform the conservation of an endangered carnivore.

The endemic island fox (*Urocyon littoralis*) of California's Channel Islands is a federally listed endangered species and has been the subject of considerable

conservation research, including a captive breeding program. Despite decades of research, significant questions remain about when foxes colonized the Channel Islands and the role that Native Americans may have played in their introduction and dispersal to six islands. Using mitochondrial genomes of 185 extant island and gray fox samples, I demonstrate that island and mainland lineages diverge ~9200-7100 cal BP and were quickly dispersed to the other Channel Islands, likely by humans. I also explore the possibility of a deliberate introduction by Native Americans using isotope data. I did not detect evidence of human resource provisioning of island foxes from early archaeological contexts as might be expected if they were introduced by ancient peoples. However, I did detect evidence of human resource provisioning on San Nicolas Island in the late Holocene and developed a long-term dataset documenting ~7300 years of foraging ecology in the endangered island fox.

Archaeological investigations of human-animal relationships through time can help document the influence of Native Americans on species distribution, abundance, and ecology. Understanding how species and humans adapted to and influenced changing environments in the past will inform decisions about protecting, preserving, and restoring biodiversity in the future. This dissertation demonstrates the importance of integrating archaeology and genomics for understanding ancient and modern human environmental relationships and modern conservation biology.

HUNTER-GATHERERS, ARCHAEOGENOMICS, AND THE EVOLUTIONARY HISTORY OF THE FOXES OF CALIFORNIA'S CHANNEL ISLANDS.

By

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Chapter 1: Introduction

Humans have been a driving force in marine and terrestrial ecosystems for millennia (Balée 2006; Crumley 1994; Redman 1999; Rick and Erlandson 2008a; Stringer et al. 2008). Throughout human history, animals have provided humans with resources and, in some cases, companionship. Humans have had complex effects on the animal kingdom, including extinction, domestication, and translocation. One of the greatest environmental impacts of ancient people was the introduction of both domestic and wild species to non-native habitats (Grayson 2001; Matisoo-Smith 2009). Globalization has led to the rapid spread of invasive species today, but the movement of species through trade networks and human migration extends back some 20,000 years and intensifies during the Holocene with the movement of domesticated species (Grayson 2001). Researchers have typically focused on the translocation of domesticated plants and animals (Larson et al. 2007; Terrell et al. 2003; Zeder et al. 2006), but wild plants and animals have received less attention (but see Flannery and White 1991; Grayson 2001). The time depth of ancient translocations of non-domesticated animals often blurs the division between the natural and cultural world and challenges ideas of "pristine" land or seascapes. Pristine landscapes do not exist due to considerable human impacts including climate change, ocean acidification, pollution, landscape clearance, and growing human populations. While conservation biology and land managers work to mitigate the effects of anthropogenic change and to restore and preserve contemporary ecosystems and organisms, looking to the past and using the archaeological record provides baselines or benchmarks of past ecosystem structure and variability and can help plan for future uncertainty(Jackson 2001; Rick and Lockwood 2013; Swetnam et al. 1999).

As challenges and threats to earth's biodiversity continue to increase, researchers are in need of new and unique datasets, including archaeological data, to help understand the long-term evolution and sustainability of ecosystems. Archaeological and genetic data are useful tools to help understand ancient and modern human-environment interactions, including domestication, species distributions and biogeography, human predation, and translocations (Anderson 2008; Bradley 2006; Braje and Rick 2011; Campos et al. 2010a; Grayson 2001; Lorenzen et al. 2011; Matisoo-Smith 2009; Rick and Erlandson 2008b). Genetic approaches have much to offer archaeologists investigating human-environment interactions, especially if the data are interpreted within a broader appreciation of the cultural landscape. This study describes a new approach to using archaeological and genetic data to inform the conservation and management of an endangered island mammal, the Channel Island fox (*Urocyon littoralis*).

The endemic island fox of California's Channel Islands is listed as a critically endangered species and has been the subject of considerable conservation research, including a captive breeding program (Coonan et al. 2010). The precise origins of the island fox are unclear, with researchers arguing for a natural, cultural, or combined dispersal (Rick et al. 2009b). Most researchers agree that Native Americans deliberately introduced island foxes from the northern to the southern Channel Islands by 5,000 years ago, and other evidence suggests that Native Americans may have first introduced foxes from the mainland to the northern Channel Islands. However, significant questions remain about the human role in the timing and the origins of this important endemic mammal and island predator.

This interdisciplinary research will enhance our understanding of the role that

humans played in shaping Channel Island ecology and biodiversity, and provide a model for other studies around the world. By dating "dispersal/introduction" events and placing them in the context of the archeological/paleobiological records using high throughput sequencing, I investigated the role of anthropogenic, biotic (introduction and dispersal of other species), and environmental factors (e.g. climate change) in shaping island fox genetic variation during the last several millennia. These data will allow us to better understand how humans have manipulated and influenced ecosystems by introducing animals to new environments, obscuring the distinction between nature and culture. Historical ecological and archaeological investigations of human-animal relationships through time can help document the structure and function of ancient and modern ecosystems, the evolutionary history of plants and animals, and provide important data for biological conservation.

Historical Ecology and Niche Construction

Historical ecology is a transdisciplinary approach to research merging many fields of study including genetics, geology, anthropology, landscape ecology, environmental biology, and agriculture, among others. It focuses on the historical landscape that has been molded and remolded by humans and natural processes over time. A product of growing concern about modern human impact on the environment and climate change, historical ecology reminds researchers that humans have been interacting with the environment throughout our species' long history (Balee and Erickson 2006; Crumley 1993, 1994; Redman 1999; Rick and Erlandson 2008b; Winterhalder 1994). Historical ecology has a number of ecological and anthropological definitions (see Balee and Erickson 2006; Crumley 1994; Rick and Lockwood 2013; Szabó 2014; Winterhalder

1994). It also has been described as framework to incorporate history in evolutionary explanations of ecology or a way to makes sense of phylogenetic systematics (Brooks 1985). The term extends back to the 1960s and is rooted in five areas of research: forest history; the *Annales* school of thought; historical geography; paleoecology; landscape history/archaeology (Szabó 2014). Historical ecology has changed considerably since then and now includes a diverse set of practitioners from archaeologists, paleontologists to ecologists and environmental historians with a number of approaches to the field.

Balée (1998) describes four postulates of historical ecology; first, humans have affected nearly every environment on the earth. Second, Balee argues that environmental destruction by humans is not inevitable. Much research has shown that humans can and have added biodiversity to their environments (Fairhead and Leach 1995; Hobbs and Huenneke 2002; Posey 1985). Third, various political, economic, and social systems yield a diverse set of impacts on the environment and similar systems do not always have the same impact. And lastly, Balee calls us to understand human cultures within their landscape and environment as "total phenomena" (Balée 1998). Fisher and Feinman (2005) suggest three other themes for the field; recursivity, landscape as palimpsest and landscape as dynamic multi-scalar entities (Fisher and Feinman 2005). Since its inception, historical ecology has been used as framework to address a variety of environmental problems and questions including heterogeneous landscapes (Balée 2006; Bjorkman and Vellend 2010; Hobbs and Huenneke 2002; Lunt and Spooner 2005), species distributions (Laliberte and Ripple 2003; MacDougall and MacDougall 2003; Matisoo-Smith 2009), patterns of human consumption (Braje and Rick 2011; Fitzpatrick and Erlandson 2009), landscape change (Lawson et al. 2005; McGovern et al. 2007;

Simpson et al. 2001; Tipping et al. 1999) and anthropogenic fire use (Bjorkman and Vellend 2010; Pyne 1998), among others.

Historical ecology is rapidly growing to address questions of how past humans influenced the environmental patterns we see today and to apply this information to restore, conserve, and protect environments for the future. Individual disciplines have worked on studying these interactions, but there is a need to tie the data together and anthropology is a suitable choice with its theoretical complexity and it is inherently "integrative and comparative, inclusive of temporal, spatial, and cultural dimensions (Crumley 1994:2)."

Niche construction offers another perspective by examining how human behavior has created the environments we see today. Animals, from ants to beavers and humans try to make their environments more habitable by modifying them in both positive and negative manners (Smith 2007). Understanding past human niche construction is difficult but clues like management of "wild" plants and animals offer insight. Human niche construction can take many forms, ranging from domestication, plant/animal colonization of the human niche, international transport of cuttings and human control of the animal reproduction in herd hierarchies to human intervention by stalling the life cycle of plants through seed storage (Smith 2007). In this framework, humans have managed both domesticates and non-domesticates as they have all been subject to human intervention through niche construction.

Terrell et al. (2003) also describe a form of niche construction, but refer to it as "domesticated landscapes". They argue that humans are part of the natural world; they do not just adapt to their environments but are also influential in constructing them.

Domesticated landscapes include more than domesticated plants and animals, and occur in hunter/gatherer populations through knowledge of the local environment. Like nature/culture, foraging is often described as opposite farming but Terrell et al. (2003) and others show that often those described as foragers have practices traditionally described as farming (Posey 1985; Terrell et al. 2003). This blurs the distinction between foraging and farming and, to an extent, the nature/culture dichotomy.

Niche construction and historical ecological approaches are useful frameworks to address the dialectical interaction between humans and the environment. Research on human impacts on the environment are complex interactions that may be difficult to tease apart, have lasting effects but can also contribute greatly to our understanding of ancient peoples and current ecosystems (Hayashida 2005). While the scale of anthropogenic environmental impacts have changed dramatically over the past 200 years, ancient peoples have had significant roles in constructed the environments we see today, even so called "pristine" ecosystems. Human action has significantly influenced plant and animal distributions during the Holocene and now the Anthropocene. Historical ecology and niche construction are important approaches for exploring how past and present human behaviors impacted species distributions, population dynamics, and evolution.

Conservation and Pristine Landscapes

Conservation biology, as a crisis discipline, has particular ideological underpinnings that have guided policy and practice. Early conservationists like Gifford Pinchot advocated environmental management for increased efficiency in the utilization of natural resources (Hughes 2009). This approach urges human control and power over nature. It fundamentally differs from the preservationist movement, founded by John

Muir, which is based on an environmental ethic and the aesthetic and spiritual value of nature (Bavington 2002; Hughes 2009). Now conservation discourse encompasses both ideologies but in the wake of the environmental crisis, they are being reconstructed to face challenging new conservation problems. This conflict between nature /culture, natural/anthropogenic, and pristine/degraded in conservation biology is essentially about change and the desire to guard against further environmental change. Allowing some change and human intervention, but not other change and intervention is a difficult line to walk for many managers.

Historical ecologists and archaeologists are addressing this problem with nature/culture and pristine/degraded wilderness (Balee and Erickson 2006; Cronan 1996; Crumley 1994; Lyman and Cannon 2004). These concepts are problematic as they can exclude humans from being part of the natural world; thus making humans separate, and less accountable for nature (Bavington and Bondrup-Nielsen 1996). By taking the humans out of nature, wilderness encapsulates the dualism of the nature /culture divide. Humans cannot be part of the wilderness because otherwise it is not wilderness as people define it. This dualism is reproduced and makes it difficult to understand how humans can sustainably be part of Nature (Cronan 1996). In the past, this ideology has led to the development of parks without people. Exclusionary policies do not take into consideration the role humans have played in constructing those environments through management practices and historical occupation.

Lyman and Cannon (2004) suggest that ecologists and conservationists alike should refer to these historical environments not as “pristine” or “natural” states but rather as historical landscapes (Lyman and Cannon 2004). They are products of their

interactions with humans and greater climate patterns and fluctuations but humans are not the sole source of environmental change (Balee and Erickson 2006). While many ecologists agree that nearly all post-Pleistocene landscapes are influenced by anthropogenic activities (Lyman and Cannon 2004), Caro et al. (2012) assert that there are several relatively intact landscapes (Caro et al. 2012). They also argue that if there is nothing that humans have not impacted, then there are no comparative baselines for restoration and humans have a reason to continue to manipulate the environment, which can impact government policies and funding for conservation. Archaeological research shows that humans have impacted most environments often deep into the human past (Redman 1999), but also that the archaeological record can be used to develop important baselines and targets for restoration and management, help establish a long-term range of ecological variability, and assist in developing desired future conditions (Lyman 2006; Rick and Lockwood 2013; Wolverton and Lyman 2012).

Prevalent in many fields, this nature vs. culture perspective suggests that humans cannot be part of the environment for it to be considered natural, suggesting there is a pre-human pristine state that we can strive to achieve. A great example of this is the ongoing invasive species pandemic. MacDonald et al. (2006) argue that the reasons conservationists abhor invasive species is not always tied to protecting biodiversity but rather "a philosophical preference for allowing natural processes to run their own course without human interference (MacDonald et al 2006:187)." They suggest that as the distinction between natural and unnatural movements becomes hazy, especially with reference to ancient movements, maintaining this philosophical position is less viable. Naturally, species are constantly changing their ranges for better resources, expanding

into new areas and interacting with existing species, possibly leading to their extinction. Human-assisted movement or range movement due to human-induced climate change makes Nature less natural to some by challenging their understandings of what Nature is and is not.

These issues become even more convoluted as we move back in time. Species that were introduced by humans to ancient environments are often considered to be endemic, native and part of the pristine landscape. This rich contradiction creates an opportunity to study the human-environment relationship in an innovative way. Research focusing on these ancient species introduced by humans, intentionally and unintentionally, is unique in that it straddles both the past and present, and biology and anthropology.

Research Questions and Goals

The goal of this study is to explore how archaeological datasets in conjunction with genetic data can be used to understand past and present human-environment interactions and help enhance the development of realistic conservation, restoration, and management goals for biodiversity in the face of future uncertainty. In chapter two, I define my approach, which I call conservation archaeogenomics, and suggest five areas in which an archaeogenomic approach can improve conservation and management. In chapters three and four, I develop a case study on the Channel Islands Fox to address three specific objectives:

Objective 1: Resolve the evolutionary relationship between island foxes and mainland grey foxes.

Objective 2: Determine the evolutionary relationships of foxes on the various islands.

Objective 3: Evaluate how island fox diet has changed through time and how humans might have influenced these patterns.

Addressing these three objectives requires the integration of genetic, zooarchaeological, stable isotope data, and AMS radiocarbon dates with cultural and environmental history.

Environmental Background

The California Channel Islands are good place to address questions about human-environmental interactions because of their long occupational history, proximity to the mainland, limited terrestrial fauna and a strong research record on island archaeology, ecology, and geology. The eight Channel Islands (Figure 1.1) are divided into the northern and southern island groups, ranging from 20 to 98 km from the California mainland. They have never been connected to the mainland during the Quaternary, have a superb archaeological record spanning nearly 13,000 years and are one of the earliest locations of human occupation in coastal North America (Erlandson et al. 2011). The

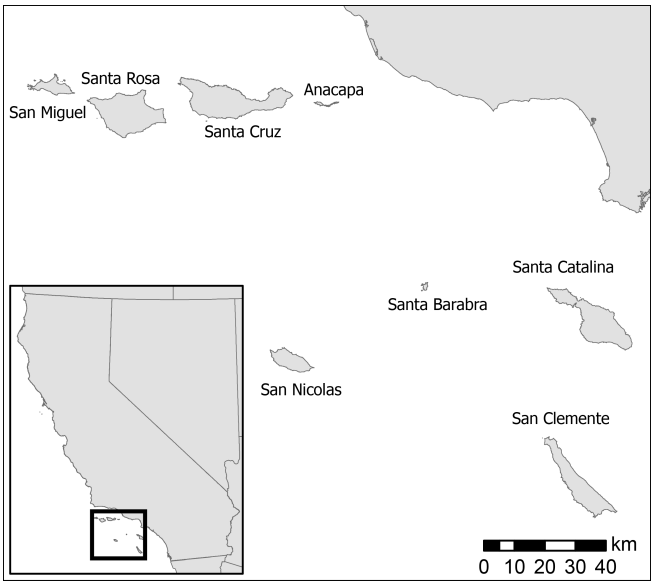


Figure 1.1. Map of the California Channel Islands. The northern island group consists of San Miguel, Santa Rosa, Santa Cruz, and Anacapa while the southern island group consists of San Nicolas, Santa Barbara, Santa Catalina and San Clemente. Map by Leslie Reeder-Myers.

Mediterranean climate (mild summers and wet winters) supports a diverse marine ecosystem, though the terrestrial ecosystem has lower species diversity than the mainland (Rick et al. 2012, 2014). The Channel Islands marine and terrestrial ecosystems also experience considerable environmental change with El Niño and La Niña effects occurring every 3-7 years and 15-30 years and are susceptible to drought and coastal erosion.

A complex combination of subsidence, volcanic and tectonic activity and uplift processes formed the geological landmasses of the California Channel Islands (Schoenherr et al. 1999). The northern islands are extensions of the Santa Monica Mountains and a deep channel separates the northern islands from the mainland. During the Pleistocene, the northern islands (Anacapa, Santa Cruz, Santa Rosa and San Miguel) formed a super-island called Santarosae that began to break-up as sea level rose around 11,000 cal BP and completed separation by 9000 cal BP (Kennett et al. 2008; Reeder-Myers et al. 2015). The southern islands were larger when sea level rose but were never connected to each other. The changing size and shape of the islands over the last 20,000 years had considerable impact on the plant, animal and people living on the islands.

The waters surrounding the islands support a diverse marine ecosystem due to upwelling at the confluence of colder (California current) and warmer currents (Southern California countercurrent) (Schoenherr et al. 1999). Kelp forests and rocky intertidal areas provide habitat for a number of marine organisms including shellfish. Large marine mammal rookeries of Northern Elephant seals (*Mirounga angustirostris)* and California sea lions (*Zalophus californianus*) are currently located on San Miguel and San Nicolas islands with smaller populations on the other islands. Current marine mammal breeding

grounds and haul-out locations differ from those in the past as a result of human activities and climate (Braje and Rick 2011). The marine ecosystems of the Channel Islands have been a critical resource for people since their arrival on the islands.

The terrestrial landscape varies by island and elevation, but is mostly coastal sage scrub, oak, pine and chaparral habitat with many endemic plants. The Channel Island terrestrial mammals (extinct and extant) are limited to ten species (excluding bats), including island fox (*Urocyon littoralis*), spotted skunk (*Spilogale gracilis amphialus*), ornate shrew (*Sorex ornatus*) and deer mouse (*Peromyscus maniculatus*), found on some or all of the islands, and several bats (Rick 2013). In the Pleistocene, pygmy and Columbian mammoths (*Mammuthus exilis* and *M. columbi,* respectively) lived on the northern islands along with a now extinct giant deer mouse (*Peromyscus nesodytes*), which may have survived until the middle Holocene (Ainis and Vellanoweth 2012; Rick 2013; Rick et al. 2012). Additionally, there are several species of herpetofauna and large populations of land and sea birds though only the island scrub-jay (*Aphelocoma insularis*) is considered endemic among the birds (Schoenherr et al. 1999). A number of plants and animals have also been introduced to the islands, including mule deer (*Odocoileus hemionus),* pigs (*Sus scrufa*), goats (*Capra hircus*), sheep (*Ovis aries*) and bison (*Bison bison*) but the vast majority have now been removed through targeted restoration actions. Today, the terrestrial and

Figure 1.2 Santa Catalina Island Fox. Island fox receiving a health examination. Photo by C. Hofman

marine ecosystems of Channel Islands are managed by a number of partner agencies including the National Marine Sanctuary, the Navy, the Catalina Island Conservancy, The Nature Conservancy, and the National Park Service.

Culture History of the Channel Islands

Chumash and Tongva peoples and their ancestors have subsisted on the islands for thousands of years. They relied on the local ecosystems for food and other resources, specifically the marine ecosystem as evidenced by large numbers of shell middens on the islands (Erlandson et al. 2011). The northern islands were historically occupied by the Island Chumash, who spoke a dialect of the Chumashan language, and the southern islands by the Uto-Aztecan speaking Tongva/ Gabrielino (Rick et al. 2005). Both groups currently reside on the California mainland, but in the past island residents were connected to mainland populations through complex social, trade and exchange networks (Kennett 2005; Rick et al. 2005).

In the terminal Pleistocene/early Holocene (13,000-7000 cal BP), people first arrived on the Channel Islands. On the northern Channel Islands, SRI-512 (12,100-11,720 cal BP), Cardwell Bluffs (12,360-11,250 cal BP), Daisy Cave (12,600-550 cal BP), and Arlington Springs (13,000-12,000 cal BP) are early paleocoastal archaeological sites contemporaneous with Clovis and Folsom sites inland (Erlandson et al. 2008a, 2011; Johnson et al. 2002; Rick et al. 2005). The southern Channel Islands and Isla Cedros have early dates of ~10,000 and 12,100 cal BP, respectively (Cassidy et al. 2004; Erlandson et al. 2008a; Raab and Cassidy 2009). Though many of the early sites are likely underwater, the record suggests that southern California peoples were using boats to colonize islands, were hunting and foraging on the water, and were sustaining long-term maritime

economies. Early Holocene economies revolved primarily around a diverse set of shellfish collecting supplemented with fish, birds, terrestrial and marine mammals, and a variety of plants (Erlandson 1994; Erlandson et al. 2008b; Reeder et al. 2008; Rick et al. 2001, 2005). There is little evidence to suggest that early coastal peoples were big game hunters (Lightfoot 1993; Rick 2013) and a growing body of data has shown that plant resources was a larger component of ancient peoples diet than previously thought (Gill 2014). Limited changes in subsistence, technology, and sociopolitical organization occurred between 9000 and 6000 years ago, while between 6000 and 3000 years ago (Moss and Erlandson 1995), there is considerable change leading up to the "classic" Chumash culture complex.

In the Middle Holocene (7000-3500 years ago), cultural, technological and environmental changes accompany variation in subsistence patterns across the Channel Islands (Glassow 1997; Glassow et al. 2012; Kennett et al. 2007; Vellanoweth 2001a). People took advantage of a diverse set of resources including shellfish, marine mammals, nearshore and kelp fisheries, birds, plants, and traded goods. Middle Holocene sites vary with some being seasonally or temporarily occupied while others were large village sites (Kennett 2005). Regional exchange networks connected mainland and island communities with the trade of Catalina soapstone, cherts, and shell beads (Rick et al. 2005; Vellanoweth 2001b). California mussels dominate assemblages on the northern islands though middens often contained large numbers of other shellfish taxa including abalone, turban snails, owl limpets, and chitons (Rick et al. 2005). Marine mammal hunting peaked during the Middle Holocene, with the most evidence coming from the southern Channel Islands (Porcasi and Andrews 2001; Porcasi and Fujita 2000). On the

northern Channel Islands, possible resource depression is evident at some sites due to size reductions in shellfish species between ~8000 and 3000 years ago, but in other sites, ancient foraging activities appear to have been sustainable over the long-term (Erlandson and Rick 2010).

During the Late Holocene (3500 cal BP-1820 AD), large dense middens and cemeteries in the northern islands and evidence of ritual sites in the southern islands suggest dramatic changes in cultural and subsistence patterns associated with the emergence of cultural complexity and the development of the plank canoe or *tomol* (Gamble 2002; Rick et al. 2005). Ranked society among the island Chumash may have appeared in the form of a chiefdom (650-750 BP) during a period of decline in marine productivity that created subsistence stress and drought (Arnold 1992, 2001). The expansion of primary villages away from top-ranked locations in the late Holocene may indicate the emergence of social stratification as villages with high population densities compete for limited resources (Kennett 2005). Subsistence patterns suggest an increase in the importance of fish, especially near shore fisheries and diminishing importance of shellfish (though more varieties) (Porcasi et al. 2000; Raab et al. 1995), likely due to population growth and the development of the single-piece fishhook (Jazwa et al. 2012; Raab et al. 1995; Rick et al. 2002, 2005). During the last 1500 years, people also increased their reliance on deepwater fish, including tuna, swordfish, mola, and mako shark (Porcasi and Andrews 2001; Rick et al. 2005), though these never represented an important overall part of the diet. The Late Holocene dependence on fishing has been linked to declining health and increasing incidences of violence suggesting increased resources stress and social stratification (Kennett 2005).

The historic period begins with the first European contact with the islands in 1542 when Spanish explorers led by Juan Rodriguez Cabrillo harbored in the Santa Barbara Channel (Kennett 2005). Gaspar de Portola's expeditions in 1769 estimated population sizes to be 8,000 to 25,000 for mainland and island Chumash (Kennett 2005). Ethnohistoric information suggests people lived in a mixed economy (with a clear division of labor) from marine resources to acorns and deer in large permanent villages though there may have been seasonal movements following food sources and water (Rick et al. 2005). They were organized hierarchally into extended matrilineal family units with villages composed of several clans though elite lineages were patrilines (Kennett 2005). There were intensive economic exchange networks documented by Spanish and supported by the archaeological record.

The Chumash remained on the islands until early 1800s when most of the inhabitants were forced into missions on the mainland (Johnson 1999a,b; Johnson and McLendon 1999). Ranchers replaced the Native Americans on the islands by the mid 1800s. Ranchers introduced deer, elk, sheep, and bison to the islands causing dramatic erosion and environmental degradation (Johnson 1980; McChesney and Tershy 1998). Simultaneously, in Channel Island marine ecosystems, intensive hunting of sea otters by Russian and Aleutian hunters led to near extermination in the early 1800s and subsequent population explosions in red abalone and sea urchin populations around the islands. In the 1860s, Chinese immigrants set up fishing camps, but primarily harvested black abalone (Braje et al. 2007). In recent times, cycles of overharvesting, environmental change and market forces closed the abalone industry in 1997.

Ownership and management of the islands has varied considerably in the 20th century from private ownership for ranching purposes to military training grounds. The US Navy began its occupation of San Miguel Island in World War II, and now jointly manages the island with the National Park Service (NPS). Additionally, the Navy operates active military installations on San Nicolas, and San Clemente. In 1980, the Congress designated Anacapa, San Miguel, Santa Cruz, Santa Barbara and Santa Rosa islands as National Park. Access to NPS islands by the general public is limited by the frequency of boats and planes and is highly coordinated to limit impact. The Nature Conservancy (TNC) owns and manages over half of Santa Cruz following a 1978 agreement with the family that owned it. The Catalina Island Conservancy owns and manages 88% of Catalina, the only island with regular inhabitants in the towns of Avalon and Two Harbors. With many different stakeholders, including the public, researchers, military, NPS, and TNC, management of the Channel Islands is a collaborative effort balancing conservation with recreation and defense. In recent years, there have been considerable efforts to restore island ecosystems to their pre-ranching form. Archaeological research has been particularly useful in this capacity in determining the form and function of earlier ecosystems and how humans influenced these ecosystems.

Human-environment interactions

Despite 13,000 years of human occupation, the emergence of social stratification, and significant population growth leading to more pressure on island resources, archaeological research has demonstrated long-term resilience and adaptation by hunter-gatherers, marine resources, and island ecosystems (Braje 2010; Erlandson and Rick 2010; Rick 2011; Rick et al. 2014). However, there have been major disturbances to

Channel Islands terrestrial ecosystems, especially with the mid-Holocene introduction of terrestrial mammals including dogs (*Canis familiaris*), possibly foxes, and the replacement of *P. nesodytes* with *P. maniculatus*. These possible translocations would have greatly impacted the terrestrial ecosystem including ground-nesting birds and marine mammal breeding grounds. Rick et al. (2009) have shown that ground-nesting birds disappear from archaeological deposits at the time foxes seem to appear.

A number of questions remain about the arrival of the island fox, by natural or cultural dispersal: How long ago did mainland foxes colonize the Islands? From where on the mainland did the founding populations originate? Have there been multiple introduction/colonization events from the mainland to the islands? What are the evolutionary relationships of foxes through time on the various islands? How has the genetic diversity of island foxes changed through time and how might humans have influenced these patterns? If humans introduced foxes to the islands, then the morphological and behavioral differences observed in island foxes could be the results of anthropogenic-mediated selection (Smith 2007; Terrell 2003). This interdisciplinary project will improve our understanding of the evolutionary history of island foxes, and the influence of Native Americans on species distribution, abundance, and ecology. Understanding how animal species and humans adapted to and influenced changing environments in the past will inform decisions about protecting, preserving, and restoring biodiversity, and help untangle issues about the inter-relationships between human cultural practices and the natural world.

Dissertation outline

This dissertation explores the ways in which ancient and modern peoples interacted with and influenced the ecosystems where they lived and how we can learn from these interactions through archaeological and genomic methods to conserve and manage the environment for the future. In chapter two, I define the field of conservation archaeogenomics and discuss five avenues of research (ancient disease ecology, extinctions, translocations, bottlenecks and ranges shifts, and reconstructing ancient environments) that can inform conservation and management with a long-term perspective. This chapter is in review at the journal *Trends in Ecology and Evolution.* In chapter three, I investigate extant genetic diversity in the Channel Islands fox and explore possible hypotheses for the origins of the island fox. I show that mitogenomes suggest rapid evolution of the island fox in less than 9000 years and likely arrived on the Channel Islands during human occupational history. This chapter is published in *PLOS One.* In chapter four, I present and analyze island fox AMS radiocarbon dates and stable isotope data to explore human-fox interactions across space and through time that will be submitted to *Quaternary Science Reviews*. In chapter 5, I discuss the broad implications of this research on the island fox and ancient translocations and future directions for exploring conservation archaeogenomics around the world.

Chapter 2: Conservation Archaeogenomics: Ancient DNA and Biodiversity in the Anthropocene

Abstract

There is growing consensus that we have entered the Anthropocene, a geologic epoch characterized by human domination of earth's ecosystems. With the future uncertain, we are faced with understanding how global biodiversity will respond to anthropogenic perturbations. The archaeological record provides a valuable perspective on human-environment relationships through time and across space. Ancient DNA analyses of plant and animal remains from archaeological sites provide a framework for understanding past human-environment interactions, which can help guide conservation decisions during the environmental changes of the Anthropocene. We define the emerging field of conservation archaeogenomics, which integrates archaeological and genomic data to generate baselines or benchmarks for scientists, managers, and policy-makers by evaluating climatic and human impacts on past, present, and future biodiversity.

Ancient DNA, Archaeology, and the Anthropocene

Throughout much of our history, humans have altered the biosphere, impacting plants, animals, and ecosystems through a variety of activities, and producing an archaeological record of human interactions with the natural world (Grayson 2001; Redman 2004; Smith 2007). Although major anthropogenic impacts on biodiversity are linked to industrialization and the modern period, ancient peoples also interacted with, and had both positive and negative impacts on, the environment. Modern ecosystems are products of this deep history, and long-term perspectives on their evolution both with and

without humans can provide important information on their capacity to withstand perturbations (Erlandson and Rick 2010; Rick and Lockwood 2013; Wolverton and Lyman 2012). The pace and scale of modern anthropogenic environmental impacts and growing recognition of the importance of investigating ancient human-environmental interactions play an important role in the Anthropocene debate, which centers around whether or not we have entered a new geologic epoch characterized by human domination of Earth's ecosystems (Braje and Erlandson 2013; Corlett 2015; Crutzen and Stoermer 2000; Smith and Zeder 2013). While researchers debate if and when the Anthropocene began, one thing that remains clear is that we need new datasets and interdisciplinary approaches to help us understand and transcend the major environmental challenges of our time, including climate change, extinction of biodiversity, emerging infectious diseases, and a host of other issues.

Here, we focus on one of these new approaches, which we call Conservation Archaeogenomics, or the genomic analysis of the archaeological remains of plants, animals, soils, and other materials to enhance present day conservation and management. Genomic approaches have become a promising tool for conservation practice, as using genome-wide data can offer a dramatic increase in the number of genetic markers that can be used to improve the precision of estimating adaptive and neutral diversity and demographic parameters of relevance. This, in turn, results in better wildlife management recommendations, including the preservation of genetic diversity, identification of populations with unique evolutionary history and potential, and the mitigation of the effects of small population sizes on viability (Funk et al. 2012; Shafer et al. 2015). While there are challenges in undertaking effective conservation genomics projects (Shafer et al.

2015), genomic analysis of archaeological samples (archaeogenomics) can extend patterns deep into the past and, along with fossil and subfossil samples (Poinar et al. 2006; Shapiro and Hofreiter 2014), can provide key information on long-term ecosystem responses to disease, human activities, and climate change (Allaby et al. 2015; de Bruyn et al. 2011; Leonard 2008; Parks et al. 2015; Willerslev et al. 2014). We focus on the following question: How can genomic analysis of archaeological materials enhance the conservation, management, and restoration of present day (and future) biodiversity? To evaluate this question, we focus on five inter-related issues of broad significance: population and distribution changes, translocation, extinction, disease ecology, and environmental reconstruction.

Conservation Archaeogenomics: A transdisciplinary approach

Conservation biologists and managers rely on baseline data when evaluating potential actions for species management and preservation, and conservation archaeogenomics has a unique role in these reconstructions (Box 1). Conservation archaeogenomics involves collaboration between archaeologists, with intimate knowledge of local and regional sites and faunal datasets (and their limitations), geneticists, with the capacity to execute methodological and analytic techniques, and managers, who make policy and management decisions. These teams can address the multiplying threats facing Earth's biodiversity by integrating novel technologies with unique datasets, including archaeological data (Figure 2.1), to study the evolution of ecosystems through space and time and evaluate their capacity to withstand human perturbations.

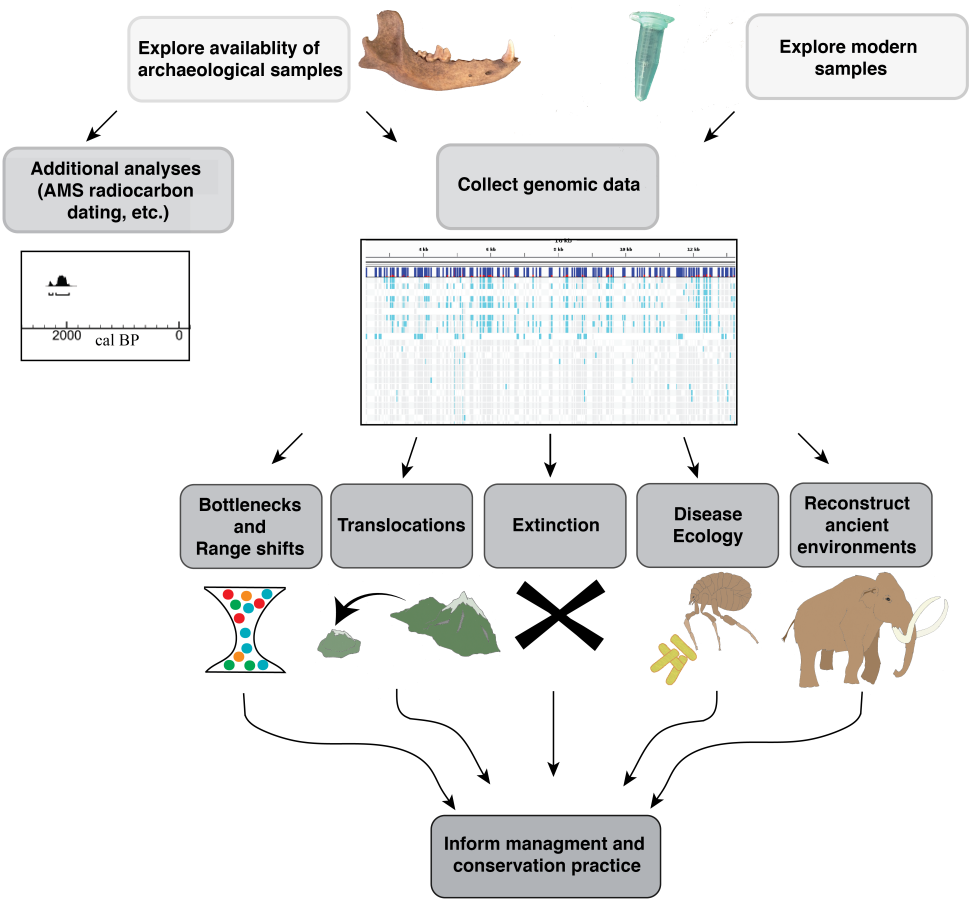


Figure 2.1. Workflow for an archaeogenomic approach to conservation.

Archaeological sites provide subsamples of past environments, as ancient peoples interacted with and used the resources that were available to them. Archaeological data can complement and enhance the natural accumulations of plants and animals represented in paleontological sites (Box 2). Although selecting sites associated with human activities may seem limiting because it does not allow the survey of an entire ecosystem, it can actually provide a powerful perspective for understanding human-ecosystem interactions. This is especially so during the Holocene where there have been major shifts in plant and animal distributions, but there is often a limited fossil/subfossil record. Archaeogenomics and paleogenomics are two complementary

approaches and much of our synthesis will highlight the inter-relationships between the two. Initially described as the study of ancestral regions of the genome and ancestral genome reconstruction (Birnbaum et al. 2000; Jurka 1994), paleogenomics is now defined as a field that aims to reconstruct past genomes through ancient DNA methods (Poinar et al. 2006; Shapiro and Hofreiter 2014). This differs from archaeogenomics, which aims to examine the direct link between humans and samples recovered in an archaeological site. Both research areas have been transformed by recent advances in ancient DNA (aDNA) methods and high-throughput DNA sequencing (HTS) technology, expanding the types of questions that can be addressed (Box 3).

Population and distribution changes

With growing climatic uncertainty and human impacts, a major concern is the reduction or loss of appropriate habitat for many taxa, forcing changes in species distributions, population bottlenecks, local extirpation or extinction (McGill et al. 2015). Although some species may be able to shift their ranges, many have specific resource requirements that might also be impacted by climatic range shifts. For example, North American birds show considerable variability in the projected range shifts under three different climate forecasts (National Audubon Society 2014). While some species may expand their ranges, others will face considerable declines. Population declines could result in reduced genetic diversity and adaptive potential, and therefore are an important focus for conservation archaeogenomic research. Archaeologists have assessed range shifts by examining temporal and spatial relative abundances of animal bones from a number of archaeological sites. When genetic data are incorporated into these studies, they can disentangle the causes of range shifts and identify their impact on genetic

diversity (Box 4), and these datasets can be compared to climate forecasts. Archaeogenomic data also provide context for interpreting changes in behavior and range as these species recover (Braje and Rick 2011; Etnier 2004).

Assessing historical genetic diversity and the time scale at which it is lost or gained is also an important part of examining the effects of long-term environmental change on biodiversity (Beadell et al. 2009; de Bruyn et al. 2011). In the case of the sea otter (*Enhydra lutris)*, genetic data from microsatellites show dramatic losses in heterozygosity and allelic diversity following the fur trade; however, otter population structure seems consistent through time (Larson et al. 2012). Interestingly, mtDNA of archaeological sea otters from Oregon showed that they were more closely related to the least genetically diverse otter population from California, rather than Alaska, where reintroduction stocks originate (Valentine et al. 2007). Studies like these demonstrate the value of archaeological samples for identifying appropriate source populations for reintroductions. Archaeogenomic data can expand these studies by providing fine-scale resolution to changes in modern and ancient population genetic structure. This can help to identify populations that have undergone dramatic loss of genetic variability or unveil evolutionarily significant units that might be in need of conservation efforts.

Identifying changes in population genetic diversity caused by anthropogenic or climate-related forces necessitates careful temporal and spatial sampling. Detecting bottlenecks statistically varies considerably depending on temporal sampling, bottleneck intensity, recovery speed, generation time, and the DNA marker used (Mourier et al. 2012). Rapid recovery and moderate bottlenecks are very difficult to detect but sampling just before and after the bottleneck increases the power of detection (Mourier et al. 2012).

Archaeogenomic data are therefore critical to detecting historical anthropogenic bottlenecks by anchoring our estimates of genetic diversity loss within human history. Data obtained from single nucleotide polymorphisms (SNPs) from archaeological herring (*Clupea pallasi*) bones have shown promise for elucidating historical population structure and anthropogenic impacts on this important fishery (Speller et al. 2012). Sequence capture methods (including SNPs) and whole genome sequencing of ancient samples have become more affordable and are useful tools to assess long-term population demographics, especially bottlenecks, in species of conservation or management concern.

Translocations

Translocations are the movement of plants, animals, or other organisms from one location to another by humans. Ancient translocations have been significant in establishing current species distributions of wild and domesticated plants and animals(Grayson 2001). Humans have moved bananas from Asia to Africa (Lejju et al. 2006), domesticated dogs across the world (Druzhkova et al. 2013; Freedman et al. 2014; Leonard et al. 2002; Pang et al. 2009; Thalmann et al. 2013), and brought pigs and chickens to the Pacific Islands (Anderson 2008; Larson et al. 2007; Matisoo-Smith 2009; Matisoo-Smith et al. 1998; Matisoo-Smith and Allen 2001; Storey et al. 2010). There are also numerous wild species that have been translocated around the world since the Pleistocene. The grey cuscus (*Phalanger orientalis),* a small marsupial, was translocated to New Ireland 19,000 years ago, to the Solomon Islands by 9000 BP, and to Timor by 4500 BP (Flannery and White 1991; White 2004). Insects (beetles, lice, fleas, and flies) were introduced to Iceland and Greenland by the Norse; various species of snails followed human migration across the Pacific; several species of hutia were transported

across the Caribbean; shrews, mice, deer, foxes, and rats have been introduced to various islands in the Mediterranean, North America, and Oceania (Grayson 2001).

Many ancient translocation studies rely on the presence of bones in assemblages, their age and association with or without humans, but a growing number of researchers are incorporating genetic information from modern samples (González-Porter et al. 2011, 2013) and a few include aDNA data. Archaeogenomic methods have been used to test a commensal model for the human settlement of the Pacific through radiocarbon dating and genetic analysis (Matisoo-Smith 2009; Storey et al. 2013). This commensal model asserts that certain animal species can be used to track the movement of people because it is likely only through human transport that these species moved to new environments. Initially extant *Rattus exulans,* the Pacific rat, mitochondrial DNA sequences showed relationships between rat populations on different Pacific islands following human settlement (Matisoo-Smith et al. 1998). To develop a chronology of this settlement, archaeological rat samples were used and additional species, including pigs and chickens were studied to examine interspecific patterns of human expansion across the Pacific (Larson et al. 2007; Matisoo-Smith 2009; Matisoo-Smith and Allen 2001; Storey et al. 2010, 2013). Commensal models have now been applied in other areas of the world, including North Atlantic translocation of house mice (*Mus musculus)*(Jones et al. 2012, 2013; Searle et al. 2009).

The introduction or translocation of plants and animals, either recent or ancient, can have considerable impacts on an ecosystem. The invasive species epidemic has demonstrated the considerable impacts of introduction events: local extirpation, trophic cascades, and extinction. Some ancient translocations had similar impacts on new

environments. The implications of ancient translocations for conservation and management, however, are complicated and intertwined with cultural values and ideals. Should prehistoric human translocations be eradicated? How long is enough time to be considered native? Is the mechanism of arrival important? Some ancient translocated species are loved while others are abhorred (Macdonald et al. 2006). How do human values and culture impact this designation? These questions show that a nuanced discussion of ancient translocations is essential when making conservation and management decisions. Any management practice including eradication, establishing captive populations, exclosures, reintroduction, genetic rescue, etc., should be carefully considered. Conservation archaeogenomics is an ideal tool for exploring baselines or restoration targets to evaluate how ancient translocations impacted ecosystem structure and function at specific time points and a starting point for discussion on how they should be managed in the future.

Extinction and De-Extinction

The dramatic loss of biodiversity in the last 200 hundred years has some researchers placing us in a sixth mass extinction event (Barnosky et al. 2011; Thomas et al. 2004; Wake and Vredenburg 2008). While extinction is a natural process, the rate of anthropogenic extinctions of certain taxa have increased dramatically during the Anthropocene (Barnosky et al. 2011; Harnik et al. 2012; Raup and Sepkoski 1982). Archaeological data can tell us when and where a species lived and potentially how it interacted with humans, allowing us to explore the timing and cause of extinctions. Archaeogenomics can help correlate changes in genetic diversity with cultural and environmental history to potentially identify cause and effect of extinction. Ancient and

more recent extinctions have also had profound implications for the structure and function of future ecosystems. The extinction of birds on Pacific islands following the arrival of humans and their commensals has had a profound impact on island ecosystems (Box 4). The study of past extinctions presents an opportunity to understand the human activities and behaviors that may have induced the extinction process. This will help us better evaluate the activities that need to be changed or minimized to reduce the risk of extinction in the future.

Archaeologists and paleobiologists have long debated the cause of the extinction of the Pleistocene megafauna. Hypotheses range from overhunting to climate change, disease, an asteroid, or a combination (Barnosky et al. 2004; Firestone et al. 2007; Grayson and Meltzer 2002, 2003; Martin 2005; Surovell et al. 2009). Archaeogenomic data are playing an important role in helping resolve the long-standing debate over megafauna extinction. These data have shown that there is not a general pattern for all megafauna extinctions; rather, there are species-specific responses to a variety of factors (Box 3) including climate change, range contraction, hunting, and encroachment by humans, and introduction of predators (Campos et al. 2010a, 2012; Lorenzen et al. 2011). Archaeo- and paleogenomic samples and species distribution modeling suggest climate change as the most likely cause of the extinction of musk ox in Eurasia (Campos et al. 2010b), while humans may have been involved in the demographic collapse of bison after 16,000 cal BP (Lorenzen et al. 2011) and a combination of causes could have led to the extinction of wooly mammoths (Lorenzen et al. 2011; MacDonald et al. 2012).

Understanding the cause, timing and impact of these extinctions remains important as re-wilding advocates have proposed introducing proxy animals to recover

the ecosystem function lost following the extinction of megafauna (Donlan et al. 2006). Recent advances in cell and molecular biology have given scientists the technological tools to aspire to bring back species that went extinct as a result of recent anthropogenic actions. This process is known as de-extinction or species revivalism. Given short fragments of degraded DNA and missing data, the first challenge to de-extinction is sequencing an ancient genome. Additional biological challenges include genome editing and developing the reproductive biology necessary for producing living animals. De-extinction would also require considerable investments in reconstructing the behavior and landscape of the extinct species, preventing disease, and protecting animal welfare. This concept is being explored by conservation biologists, journalists, ethicists, and other scientists (Jørgensen 2013; Sherkow and Greely 2013; Zimmer 2013), but it is highly controversial and poses many challenges, both biological and ethical.

Ancient Disease Ecology

Emerging infectious diseases pose serious public health concerns and are a considerable threat to biodiversity through changing host-pathogen biology and biogeography (Daszak et al. 2000). During the past few decades, dramatic human population explosion, rapid global expansion of transportation networks, and accelerating climate fluctuations have acted together to increase the frequency of emerging diseases, but this phenomenon is not restricted to recent human history. A growing body of aDNA research examines ancient disease transmission and evolution. Archaeological and genetic research on ancient human disease has yielded considerable data on the impact of diseases such as tuberculosis on human populations (Harkins et al. 2015; Wilbur et al. 2009), but also the evolution and movement of the disease agent to the New World (Bos

et al. 2014). Zoonotic bacteria and other infectious bacteria have been detected in ancient human dental calculus microbiomes (Warinner et al. 2014) and could also be studied in faunal calculus samples to examine transmission between humans and wildlife. Past and present disease outbreaks in wildlife and humans, pathogen evolution, and the human role in the emergence and movement of diseases can also be explored with archaeogenomic data.

The influence of disease on wildlife and domestic animals can also be explored in archaeological materials. Infectious diseases can have significant impacts on populations, and species of conservation concern can be highly susceptible to disease outbreaks as small effective population sizes limit adaptability. For example, ancient Tasmanian devils show low MHC diversity that might contribute to their susceptibility to a contagious facial cancer (Morris et al. 2013). Archaeological and genomic resources present good opportunities to evaluate whether taxa have been exposed to disease in the past, how they responded, and how they might respond in the future. New methods that utilize sequence capture for detecting particular diseases (Bos et al. 2015) have provided reliable tools for investigation of ancient disease dynamics. Bos et. al (2011) applied sequence capture and an archaeogenomic approach to confirm that the cause of the Black Death was the bacterium *Yersinia pestis*. They also examined the evolution of this zoonotic disease transmitted to humans by fleas carried by rats (Bos et al. 2011). This strain appears ancestral to modern strains, suggesting that the transmission of the Black Death across Europe contributed to the distribution of all pathogenic *Yersinia pestis*. Depending on DNA preservation and disease biology (e.g., transmission, progression, symptomatology,

host specificity, etc.), animal hosts or commensal animals might be additional sources of information on pathogen transmission and evolution.

Museum samples fill important time gaps between archaeological collections and the present when examining long-term patterns, including pathogen evolution and transmission. Museum genomics has confirmed the presence or absence of particular pathogens, allowing us to trace the spread and understand the demographic impacts of disease. Koala museum skins have been used to reconstruct 130 years of rapid evolution in koala retrovirus, which is in the process of invading the koala genome and may be tied to declines in some parts of Australia (Ávila-Arcos et al. 2013; Tsangaras et al. 2014). In humans, archived human medical specimens have been used to reconstruct the genome of the cholera strain responsible for an 1849 Philadelphia outbreak (Devault et al. 2014). These studies are valuable because museum collections, their field records, and historical demographic data can test theory and develop methodology that can be applied to older, more degraded archaeological samples.

Reconstruction of ancient environments

Understanding how paleo-ecosystems functioned during periods of climatic instability or in response to environmental conditions similar to predicted future environments will be useful for making decisions about the future. Historical ecologists, including archaeologists, have approached environmental reconstruction by integrating faunal abundances with climatic data from geological cores. Our ability to reconstruct paleo-vegetation was historically limited to identifiable botanicals recovered in archaeological sites, and pollen cores of lakes or ponds, which are geographically confined. Ecological niche modeling of paleo-ecosystems has filled in some of these gaps

but archaeogenomic approaches have great potential for reconstructing vegetation and ecosystem history.

New developments in metagenomics and environmental DNA (eDNA) technologies have provided the tools to detect traces of ancient animals and plants from stratified soil samples i.e. “Dirt DNA”, to reconstruct these paleo-ecosystems (Andersen et al. 2012; Boessenkool et al. 2014; Giguet-Covex et al. 2014; Hebsgaard et al. 2009; Willerslev et al. 2014). These methods help address questions of population continuity, migration, or ecosystem structure and evolution. Using both archaeological and eDNA datasets, 50,000 years of arctic vegetation history shows that plant communities may have changed dramatically in response to climate change and potentially due to the loss of large herbivores (Willerslev et al. 2014). In another study, ancient eDNA from high altitude tropical cores reflect the local vegetation, while traditional methods examining pollen may represent a broader geographic region (Boessenkool et al. 2014). Advancements in eDNA technologies have led to positive developments for reconstructing vegetation and landscape histories by facilitating recovery of highly degraded DNA from archaeological plant remains which are often found fragmented or burnt (Brown et al. 2015).

Archaeogenomics provides vast potential to investigate reintroduction locations for endangered or threatened taxa with limited ranges. Considerable environmental change between locations within a historic range and the current range can decrease the success of species reintroductions. Environmental DNA sampling of soils and archaeological sites can tell us how different the current environment is from the past and help predict reintroduction success. When integrated with archaeogenomic data on local

extinctions and historic ranges, especially if historical ranges are unknown, we can determine the timing and the potential reasons for the disappearance of the species from the landscape. Reconstructing paleo-ecosystems is a synthesis of ancient plant and animal interactions, from historic ranges to human mediated translocations, and ancient pathogens, and together can generate a more complete picture of how ecosystems have changed during considerable climatic and anthropogenic variation.

Conservation Archaeogenomics and the Anthropocene

We have described how archaeogenomics can generate data with direct implications for conservation and management decisions today and in the future. Genomic analysis of archaeological materials improves our understanding of historic ranges and bottlenecks, and can suggest appropriate source populations for reintroduction of locally extirpated populations.

Archaeogenomic data can also detect ancient translocations, their impact on ecosystems and generate baseline data on ecosystem change. Through the study of climate-induced, anthropogenic, recent, and ancient extinctions, we can better understand the risks, causes, and effects of extinctions to change human behavior and mitigate human impacts. Archaeogenomics of disease can identify ancient vectors and hosts, and explore susceptibility to diseases in ancient wildlife and human populations. These investigations allow us to reconstruct ancient ecosystems and evaluate how different the past, present and future ecosystems are from each other as we plan for the conservation, management, and restoration of local and global ecosystems.

Ongoing and impending changes during the Anthropocene situate archaeologists, paleobiologists, and others well to help address the rapidly changing environmental crisis

by adding a historical perspective to debates on appropriate baselines and human impacts. Archaeogenomic data can fill the gaps in our knowledge of historic and prehistoric environments and document ranges of ecological variability. In the past, aDNA studies of archaeological materials suffered from limitations associated with PCR methods and were greatly limited by issues of scale (sample sizes, data recovery, etc.); however, advances in genomic technologies have transformed the types of questions that can now be addressed. These developments have made archaeological samples an invaluable source of information on the changes in spatial and temporal distributions of plants, animals, disease, and ecosystems. Conservation archaeogenomics will be a useful framework for researchers and managers alike in their efforts to protect and preserve biodiversity as we prepare to face an uncertain future.

Box 1: What is Natural?

A key question in conservation and restoration is: What is natural (Willis and Birks 2006)? Managers rely on baselines that serve as targets for restoring an ecosystem or organism. However, ecological baselines can change dramatically through time and the perception of "what is natural" can be heavily influenced by past human activities and changing generational perceptions. This is called "shifting baselines" (Pauly 1995).

The shifting baselines paradigm illustrates the need for historical perspectives in conservation (historical ecology), as data from paleobiology, archaeology, history, and related fields can provide important perspectives on ecological change through time (Rick and Lockwood 2013). Rather than historical baselines serving purely as restoration goals or targets—some of which may be unobtainable or undesirable—they also can illustrate ecosystem responses to a variety of different climatic conditions and

anthropogenic influence. These long-term perspectives help establish desired future conditions and forecast future ecosystem and organismal responses to Anthropocene climate change and human activities.

Genomics plays a key role in historical ecology and establishing baselines and targets for restoration. With the ability to determine genetic patterns in the past and present, document bottlenecks, and make connections between genetic diversity and population structure, genetic analysis of archaeological and paleontological samples offers a framework for constructing baselines. These archaeogenomic data transcend simplistic notions of restoring a landscape to its "natural state" and instead document change through time and ecological variability, and make us better prepared for the conservation challenges of the Anthropocene.

Dramatic differences between the prehistoric and modern abundance of Guadalupe fur seals (GFS, *Arctocephalus townsendi*) and northern elephant seals (NES, *Mirounga angustirostris*) on California's San Miguel Island provide an example of shifting baselines (Rick et al. 2009a, 2011b). Both species were pushed to the brink of extinction during the 19th and early 20th century fur and oil trade, but have recovered dramatically since then. However, the abundance today does not match the prehistoric abundance documented in the archaeological record. NES dominate today but were rare during the past 3000 years; conversely, GFS are rare to absent today but were very common prehistorically (Figure 2.2). Genetic analyses of NES and GFS suggest that they were both more genetically diverse prehistorically than today (Hoelzel et al. 2002a; Weber et al. 2000, 2004a,b) but future, more detailed, archaeogenomic analyses could

provide greater insight into this discrepancy and how it might help us manage for global change in the Anthropocene.

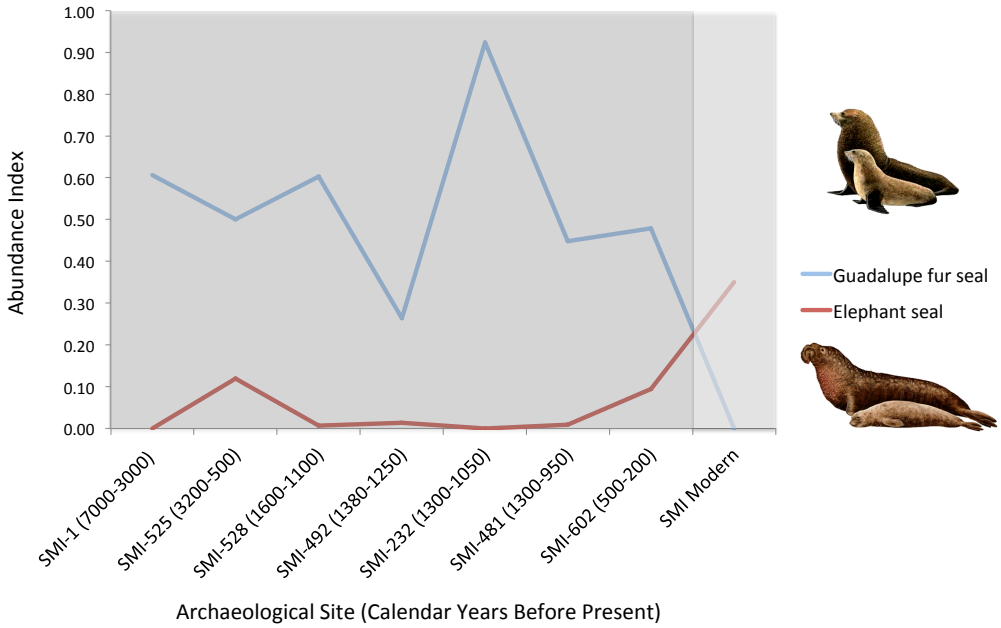


Figure 2.2 Archaeological and modern abundance of Guadalupe fur seal (GFS) and Northern elephant seal (NES). Data available in Rick et al. (2009, 2011). Note the greater prehistoric abundance of GFS and greater modern abundance of NES in archaeological sites through time.

Box 2: The Archaeological Record

Archaeologists study the material record left behind by past peoples. This record is an amalgamation of environment, people, and culture. Past peoples intentionally created a record of their activities by building structures, writing histories, and burying human and animal remains and associated valued artifacts. In addition, they unintentionally deposited ecofacts as waste including shellfish, bones, broken tools, plant remains, stone and pottery into middens. Many archaeologists focus on ancient garbage

by digging in midden and privy sites because it can tell us a lot about what was valued, used and not used by particular groups of people.

Inherently interdisciplinary, archaeologists use a variety of tools to interpret human behavior including methodologies adopted from other disciplines like stable isotopes, proteomics, and genetics. There are also several sub-specialties within archaeology including geoarchaeology, zooarchaeology, paleobotany and historical archaeology that have unique methods. For example, zooarchaeologists are experts in animal morphology and are able to estimate the number of individuals and proportions of a given animal in a site. Provenience, or the location within a site and association with other archaeological materials, is critical for interpreting a site. For instance, a bone found in a burial was likely intentionally placed there and had some significance to the person that did so. This differs considerably from a bone found in an ancient midden. These data can be compared within layers of a site, between sites, and for different species in conjunction with botanical, geological, and other data to make interpretations about culture and human behavior.

Scores of archaeological sites around the world have been excavated yielding artifacts and ecofacts for archaeogenomic analysis. Archaeological sites themselves come in a variety of sizes and types. From a campsite occupied for a single night to civilizations spanning thousands of years, the materials recovered from a site tell a story about the people that occupied it. These materials can come from a variety of site contexts including middens, caves, storage structures, houses, harvest sites, and others (Figure 2.3). Samples for archaeogenomic analysis might include animal bones, teeth, dental calculus, plant remains, soil samples, and paleofeces. Depending on the local soil,

deposition conditions, and climate, the preservation of organic remains for analysis can vary within a site and across a landscape and not all artifacts/ecofacts are suitable for DNA analysis. However, there are many great collections available for study in museums around the world.

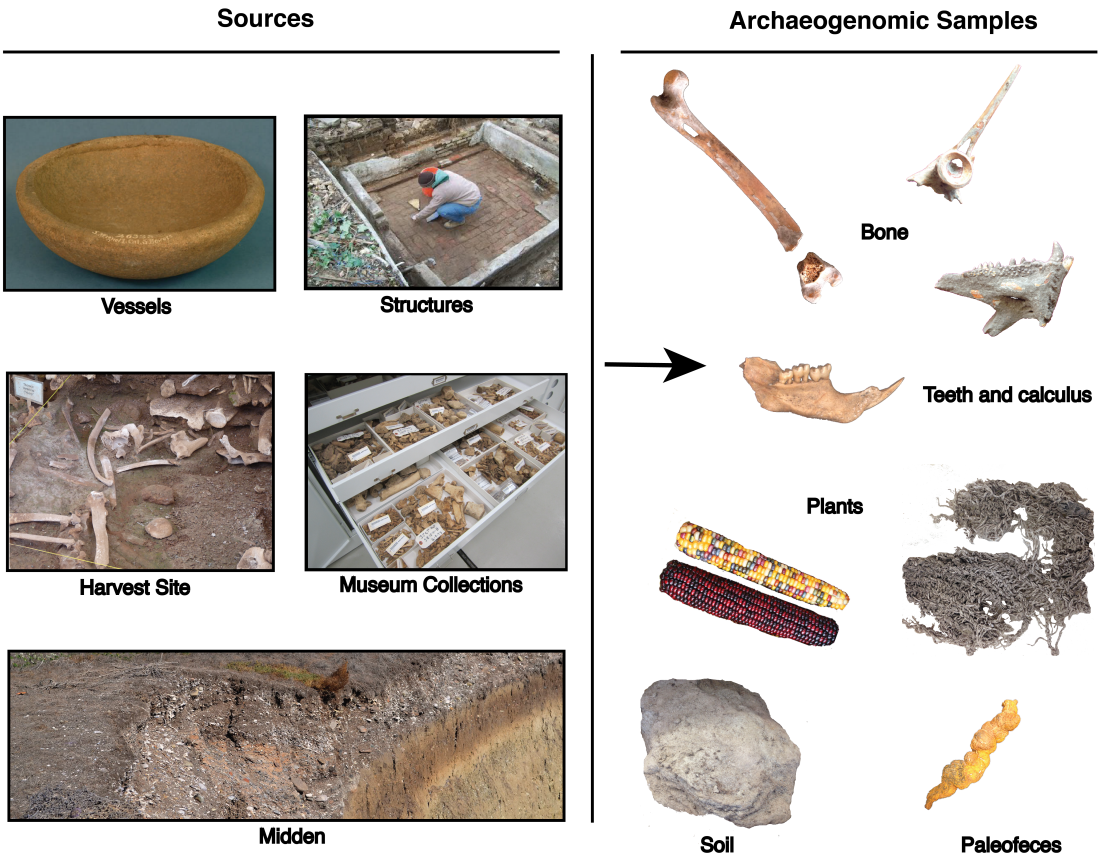


Figure 2.3. Archaeogenomic samples recovered from different contexts. Archaeogenomic samples can include bone, teeth, plant remains, soil and paleofeces, and other materials. These materials can be recovered from ancient structures, middens, storage vessels, harvest sites, caves, or from existing museum collections. Harvest site image adapted from Wikimedia commons.

Box 3: Archaeogenomics Methods - New and Old

Like genomics, ancient DNA (aDNA) has changed rapidly with the advent of high-throughput sequencing (HTS) technology. Due to the existence of relatively few samples and limitations on destructive analyses, early aDNA studies focused on

evolutionary relationships and bottleneck detection; however, with HTS technology, it is now possible to study ancient population dynamics and landscape genetics(de Bruyn et al. 2011; Parks et al. 2015). There are now also many different ways of collecting genomic data from fresh tissues including RAD, exome, intron and whole genome sequencing as well as SNP capture. However, when comparing modern and archaeogenomic data, genomic markers must be selected not only for their informativeness and resolution power but also for their successful applicability to degraded samples. While mtDNA has been the marker of choice in ancient DNA studies due to its ease of recovery in old and degraded samples, high variability, matrilineal inheritance and haploidy (Ho and Gilbert 2010; Ramakrishnan and Hadly 2009), SNPs offer higher power to detect bottlenecks, especially those with fast recoveries(Mourier et al. 2012). The feasibility of a particular project will depend on the goals, scale (i.e., number taxa and samples) and budget. Furthermore, these new genomic approaches are best used in concert with other data that can improve the context and chronology of a particular sample and can be guided by specific procedures and analysis of morphology, proteomics, AMS radiocarbon dating, isotopes, and other techniques (Figure 1). Together these datasets can be integrated to explore human impacts on biodiversity and to inform conservation and management for the future.

Box 4: Exemplar case studies

Case Study A: In a large study on six different herbivores, 846 radiocarbon dated mtDNA sequences, 1,439 directly-dated faunal remains and 6,291 radiocarbon dates associated with human occupation from sites around the world, all taxa showed dramatic range contractions from the terminal Pleistocene to the early Holocene (Lorenzen et al.

2011). Four species (horse, reindeer, bison and musk ox) show positive correlation between range size and genetic diversity through four time points. When demographic changes are compared to environmental history, archaeological abundance data and radiocarbon dates, climate change rather than human hunting is suggested as the likely cause for the demographic changes in horse, reindeer, and musk ox. Data like these show that climate change can have significant effects on the ranges and the demographics of plants and animals and we should be concerned for how future fluctuations will impact wildlife populations, especially those with already limited ranges or low genetic diversity.

Case Study B: One of the best documented and most dramatic anthropogenic extinctions is that of Pacific island birds (Olson and James 1982; Steadman 1995, 2006; Szabo et al. 2012). An estimated 2000 species went extinct following the human expansion across the Pacific islands (Steadman 1995). Whether due to introduction of commensal/invasive species like the rat or to anthropogenic landscape change (Steadman 2006; Szabo et al. 2012), the extinction of endemic island avifauna has transformed island ecosystems. In Hawaii, genetic analysis of the endangered Nene (*Branta sandvicensis*) from paleontological, archaeological, historic and extant samples show considerable loss in mtDNA variation following human colonization (Paxinos et al. 2002a). While many other Hawaiian geese and other birds went extinct during this period (Olson and James 1982; Paxinos et al. 2002b), the Nene survived, potentially as a result of intentional or unintentional cultural practices protecting the species (Paxinos et al. 2002a). However, the endangered Hawaiian Petrel (*Pterodroma sandwichensis*), the most abundant seabird in the pre-human islands, and presumed extinct by the mid 20th

century, was found from comparison of DNA sequences of 100 archaeological and paleontological subfossil bones to have retained significant levels of its historical genetic diversity in surviving present day populations (Welch et al. 2012). The long generation time of the species and its ability to "hide at sea" may have allowed a larger effective population size and greater retention of genetic variability. The 20th century observed population decline correlated with a change in isotope values suggesting a trophic shift from large to small prey items, likely a result of fishery depletion in the Northeast Pacific (Wiley et al. 2013).

Glossary Box:

Archaeology: Study of the human past using material remains.

Ancient DNA (aDNA): DNA extracted from non-living sources including teeth, bones, toepads, desiccated tissue, seeds, plant remains, and paleofeces.

Anthropocene: The period of time when humans dominated the earth's landscape.

Archaeogenomics: Utilizing materials from archaeological sites to generate genomic information.

Artifact: An object modified by humans.

Historical Ecology: The interdisciplinary study of past ecosystem dynamics.

Ecofact: An organic object found in an archaeological site including plant and animal materials.

Environmental DNA (eDNA): DNA obtained from environmental samples including soil or water.

Midden: Ancient trash deposits, often containing shells, bones and plant materials.

Paleogenomics: The study of past genomes using ancient DNA methods.

Paleofeces: Ancient feces from humans or animals. This differs from coprolites, which are fossilized feces.

Provenience: Location of an object within a site and in relation to other artifacts and ecofacts.

Shifting baselines: The concept that what we view as natural changes through time.

Chapter 3: Mitochondrial genomes suggest rapid evolution of dwarf California Channel Islands foxes (*Urocyon littoralis*)

Abstract

Island endemics are typically differentiated from their mainland progenitors in behavior, morphology, and genetics, often resulting from long-term evolutionary change. To examine mechanisms for the origins of island endemism, we present a phylogeographic analysis of whole mitochondrial genomes from the endangered island fox (*Urocyon littoralis*), endemic to California's Channel Islands, and mainland gray foxes (*U. cinereoargenteus)*. Previous genetic studies suggested that foxes first appeared on the islands >16,000 years ago, before human arrival (~13,000 cal BP), while archaeological and paleontological data supported a colonization >7000 cal BP. Our results are consistent with initial fox colonization of the northern islands probably by rafting or human introduction ~9200-7100 years ago, followed quickly by human translocation of foxes from the northern to southern Channel Islands. Mitogenomes indicate that island foxes are monophyletic and most closely related to gray foxes from northern California that likely experienced a Holocene climate-induced range shift. Our data document rapid morphological evolution of island foxes (in ~2000 years or less). Despite evidence for bottlenecks, island foxes have generated and maintained multiple mitochondrial haplotypes. This study highlights the intertwined evolutionary history of island foxes and humans, and illustrates a new approach for investigating the evolutionary histories of other island endemics.

Introduction

The origin of island endemism has long been an important topic in biogeography (Darwin 1859; Foster 1964; MacArthur and Wilson 1967; Wallace 1855) and has implications for species management and conservation. Small populations of island endemic taxa are often at risk of extirpation or extinction due to their reduced genetic diversity and increased susceptibility to genetic drift, disease, and climate change, especially in conjunction with over-exploitation, habitat loss, and predation or competition from invasive species (Diamond 1975; Frankham 1998; Lacy 1987; MacArthur and Wilson 1967). Island taxa typically experience substantial morphological and behavioral changes following dispersal and a period of isolation from the mainland (Foster 1964). Stepping-stone and other models have been proposed for the natural dispersal of a variety of taxa, but lessons from the invasive species pandemic of recent centuries suggest that ancient human introductions also may have been important dispersal mechanisms (Grayson 2001; Matisoo-Smith 2009). Because the evolution of many island taxa have been influenced by a combination of natural and anthropogenic dispersal events, distinguishing between these mechanisms requires archaeological, paleontological, and genetic data (Grayson 2001; Matisoo-Smith 2009; Storey et al. 2013). Understanding how island taxa evolved and adapted to their new environments can also improve our ability to manage island endemics in the face of rapid environmental change.

To investigate the mechanisms that generate island endemism, we studied the origins and evolution of the island fox (*Urocyon littoralis;*1-3kg), a diminutive canid endemic to six of California's Channel Islands, and a congener of the gray fox (*U.*

cinereoargenteus; 3-7 kg) found throughout mainland North America. The island fox is the largest endemic post-Pleistocene land mammal and a top predator on the Channel Islands. The recovery of fox populations on several islands following collapses due to predation and disease is among the great success stories of island restoration ecology (Coonan et al. 2010; Roemer and Donlan 2004, 2005). Previous genetic research of modern island foxes and chronological and distribution analysis of island fox remains from paleontological and archaeological contexts posed different hypotheses about fox origins on the Channel Islands (Aguilar et al. 2004; Collins 1991a,b, 1993; Gilbert et al. 1990; Goldstein et al. 1999; Rick et al. 2009b; Vellanoweth 1998; Wayne et al. 1991). In one model, island foxes diverged from California gray foxes >16,000 years ago (prior to the arrival of humans) after rafting to the northern islands and were subsequently moved to the southern islands >5000 years ago by Native Americans (Aguilar et al. 2004; Gilbert et al. 1990; Goldstein et al. 1999; Wayne et al. 1991). However, the fox remains used to support a Pleistocene divergence as much as 40,000 years ago were recently dated via Accelerator Mass Spectrometry (AMS) ^{14}C to 1480–1280 cal BP (calibrated calendar years before present) (Rick et al. 2009b). The earliest AMS dates for island foxes are now only ~ 7000 cal BP, some 6,000 years after people first arrived on the Channel Islands at ~13,000 cal BP (Erlandson et al. 2011). These data raise the possibility that island foxes may have arrived on the islands later than previously thought, diverged very recently, and undergone rapid evolution.

The eight California Channel Islands are divided into northern and southern groups situated 20 to 98 km offshore (Figure 1). The islands have an archaeological record spanning ~13,000 years, one of the earliest coastal human sequences in North

America (Erlandson et al. 2011). Sea level models suggest that the islands were larger and closer to the mainland and each other during the terminal Pleistocene and early Holocene but, throughout the Quaternary, they were always separated from the mainland by a watergap of at least 7 km (Erlandson et al. 2011; Kennett et al. 2008). During the last glacial maximum, the northern islands (Anacapa, Santa Cruz, Santa Rosa, and San Miguel) formed a super-island called Santarosae that began to separate as sea level rose ~11,000 cal BP, and were completely separated by 9000 cal BP (Kennett et al. 2008). Although the southern islands (San Clemente, San Nicolas, Santa Barbara, and Santa Catalina) increased in size during Quaternary glacial periods, they are more widely dispersed and were never connected to each other or the mainland during this time. These fluctuations in island size and distance from each other and the mainland influenced colonization and extinction rates of island taxa. As a result, the Channel Islands have several rare endemics, lower species diversity than the

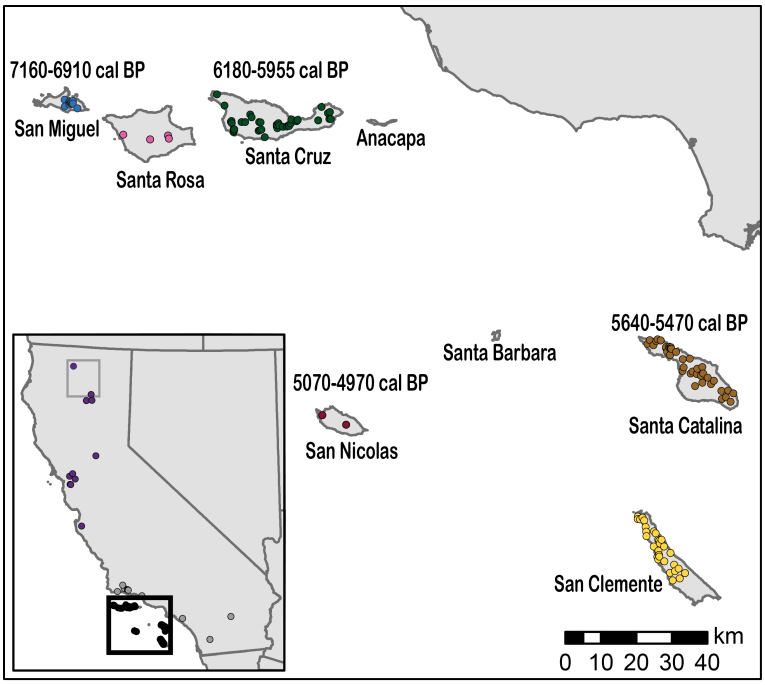


Figure 3.1. Sampled Localities of Island and Mainland Foxes. Mainland foxes were sampled from northern and southern California and island foxes were sampled from every island where they occur. The earliest directly AMS ^{14}C dated island foxes are indicated. The two gray foxes most closely related to the island fox lineage in this study are enclosed in the gray box on the inset map.

mainland, and only 10 known species of terrestrial mammals (excluding bats) (Rick et al. 2012).

Decades of research on island fox morphology and interactions with humans have documented their smaller size relative to mainland gray foxes, the occurrence of intentional island fox burials, and the use of fox pelts by Native Americans (Collins 1991a,b, 1993; Rick et al. 2009b; Vellanoweth 1998), but their evolutionary history has remained unresolved. Previous genetic research, using microsatellites, mtDNA restriction digests, allozymes, MHC, and DNA fingerprinting, primarily focused on island fox genetic variation and divergence between islands (Aguilar et al. 2004; Gilbert et al. 1990; Goldstein et al. 1999; Wayne et al. 1991). A recent phylogenetic analysis of the Canidae suggests that island and gray foxes are sister taxa (Lindblad-Toh et al. 2005), and earlier genetic analyses assigned gray foxes as an outgroup to island foxes (Goldstein et al. 1999; Wayne et al. 1991). To date, the only phylogeographic study of gray foxes was conducted on populations in the eastern United States (Bozarth et al. 2011). However, the phylogeographic patterns between eastern, western, and island *Urocyon* populations had not been determined.

Mitochondrial DNA is a powerful marker for dating mammalian divergences and mitogenomes and has been used to examine both phylogeographic and evolutionary relationships in wild and domesticated animals, including canids (Achilli et al. 2012; Gilbert et al. 2008; Lindqvist et al. 2010; Morin et al. 2010; Thalmann et al. 2013). Here, we present the first application of high throughput sequencing (HTS) of whole mitochondrial genomes (mitogenomes) to evaluate the phylogeographic patterns of differentiation between island and mainland gray fox populations. Our goal is to

reconstruct the evolutionary history of island and gray foxes and to unravel their patterns of colonization into the Channel Islands. We address the following questions: 1) When did foxes reach the Channel Islands? 2) How have human activities and climatic changes influenced their genetic diversity and the geographic distribution of genetic lineages? 3) How can these data inform our understanding of the processes leading to island endemism?

Results

Genetic Variability

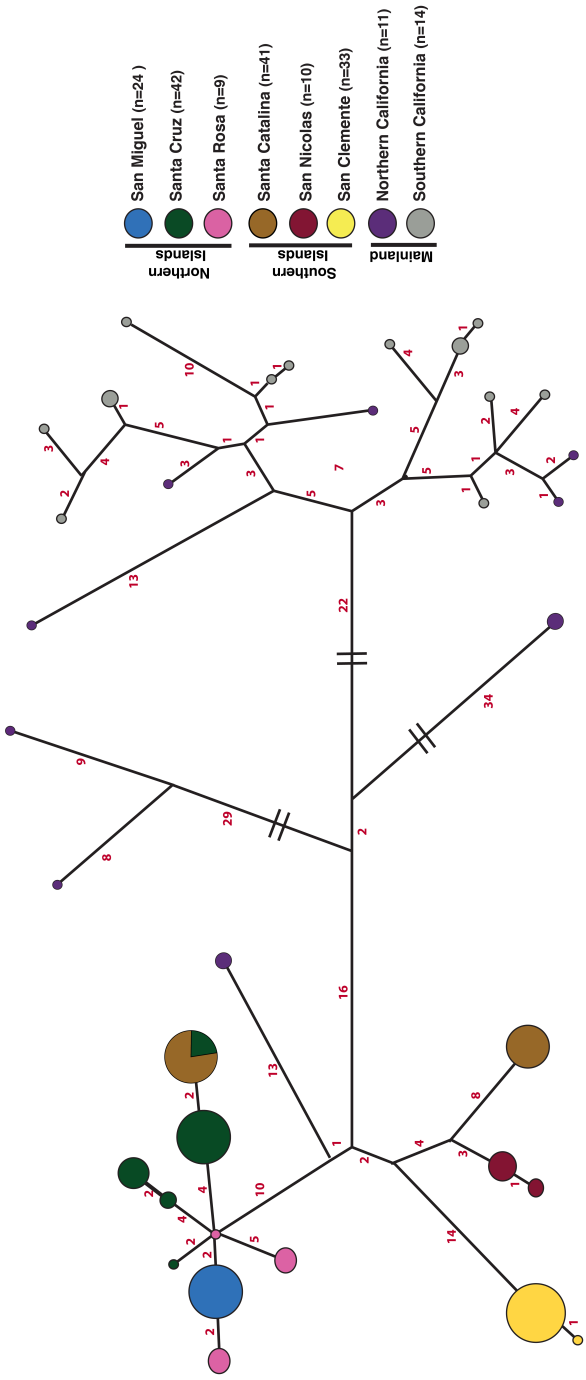
We sequenced complete mitogenomes from 159 modern (2007-2013) island foxes from the six islands in their current range and 25 gray foxes (1996 -2013) from across California (Figure 3.1 and Table 3.1). De Novo assembly revealed a 16,718 bp gray fox

Table 3.1. Mitogenome Haplotype Summary

Locality	N	Haplotypes	Haplotype Diversity	Nucleotide Diversity
San Miguel	24	1	0	0
Santa Rosa	9	3	0.667	0.0003
Santa Cruz	42	5*	0.6	0.00024
Santa Catalina	41	2*	0.51	0.00099
San Nicolas	10	2	0.356	0.00002
San Clemente	33	2	0.061	0
All Islands	***159***	***14***	***0.865***	***0.00113***
Northern California	11	9	0.964	0.00342
Southern California	14	12	0.978	0.00125
Mainland	***25***	***21***	***0.987***	***0.00248***
Virginia	1	1	-	-
Total	***185***	***36***	***0.9***	***0.00198***

* Santa Catalina and Santa Cruz are the only islands that share a haplotype.

mitogenome with a mean read depth of 171x. However, a short fragment (248 bp) of the D-loop was excluded from all subsequent analyses due to problems with assembly and



mapping of repetitive regions, leaving an alignment of 16,470 bp for all foxes. Mean read depth for all samples ranged from 33 to 7898x (std. deviation of 16 and 204, respectively) (Appendix A, Table S1). We excluded samples with conflicting or incomplete mitogenomes from analysis (n=16), yielding 185 complete mitogenomes.

Figure 3.2 Median-Joining Network of Island and Mainland Mitochondrial DNA. A Median joining network using the variable sites of the mitochondrial genome was generated in the program Network v.4.612. The size of the circles and branch lengths are proportional to number of individuals represented and the number mutations between haplotypes (red), respectively. Hash marks indicate shortened branches. Santa Catalina and Santa Cruz are the only islands that share a haplotype, which is more closely related to the northern island haplotypes than the southern.

The mitogenome sequences revealed a total of 35 haplotypes with 14 found exclusively on the islands and 21 found only in mainland California. Haplotype and nucleotide diversity in the island populations was markedly lower than in the mainland populations, with only one to five haplotypes per island. The northern islands had nine closely related haplotypes while the southern islands had five haplotypes that

were more distant from each other (Figure 3.2). All of the islands had a least one private haplotype, but 19 of 41 Santa Catalina foxes (southern island) shared a haplotype with Santa Cruz foxes (northern island). No other islands shared a haplotype, although San Clemente and San Nicolas each had two haplotypes that were separated by a single base pair. Independent analyses of two of the most widely used mtDNA genes in mammalian phylogeography, cytochrome b and D-loop, recovered only 15 and 20 haplotypes, respectively, instead of the 35 haplotypes recovered by sequencing whole mitogenomes (Appendix A, Table S2). These two genes represent a reduced portion of the genetic variation of island and mainland foxes as demonstrated by single-gene median joining networks (Appendix A, Figure S1); thus, they provide insufficient resolution to accurately investigate the colonization patterns from the mainland. Across the entire mitogenome, island foxes showed a three-fold reduction in the proportion of variable sites compared to mainland gray foxes (Appendix A, Table S2).

To evaluate the patterns of selective pressures acting on mainland and island fox mitogenomes, we estimated the proportion of nonsynonymous (dN) and synonymous variable (dS) sites throughout all of the protein-coding genes (Table 3.2). Although elevated dN/dS is a common metric for evidence of selection when comparing single genes, dN/dS values are much lower for signatures of selection across the entire mitogenome (Moray et al. 2014). Using the SLAC algorithm implemented in HyPhy (Delport et al. 2010), the island group had a substantially higher mean dN/dS ratio (0.40) than mainland only (0.10), suggesting a signal of positive selection or the relaxation of selective forces associated with a decline in effective population size (Ohta 1992).

Table 3.2: Nonsynonymous and Synonymous Substitutions

		Non-synonymous	Synonymous	Mean dN/dS
Island Only	Number of Sites	8500.49	2785.51	0.40
	Number of Variable Sites	22	27	
	Proportion of Varied Sites	0.0026	0.0097	
Mainland Only	Number of Sites	8497.41	2788.59	0.10
	Number of Variable Sites	29	148	
	Proportion of Varied Sites	0.0034	0.0531	

Chronological analysis

Archaeological and paleontological research has identified more than 100 fox bones from more than 35 different archaeological and subfossil sites across the archipelago. Many of the bones have relatively secure associated radiocarbon ages; all of which are more recent than 7200 cal BP (Collins 1991a,b; Rick et al. 2009b). Morphological analysis of these ancient bone samples indicate the characteristic island fox morphology, even in the oldest sites (Collins 1991a). To investigate the antiquity of foxes on the Channel Islands and improve radiocarbon chronologies, we obtained three new AMS radiocarbon dates of island fox bones from the potentially earliest archaeological contexts to complement previously published AMS dates. This yielded a total of nine directly radiocarbon dated ancient fox bones (Appendix A, Table S3). The earliest fox AMS radiocarbon estimates date to 7160-6910 cal BP on the northern islands (San Miguel) and to 5640-5470 cal BP on the southern islands (Santa Catalina). We found no fossil or archaeological evidence of foxes on any of the Channel Islands prior to

7160 cal BP. Our AMS dated samples show phenotypic characteristics of island foxes (i.e. smaller size), though these bones are fragmentary. Fox bones with the characteristic gray fox morphology have been recovered from relatively few archaeological sites on the coastal mainland; none have been recovered on the Channel Islands. Similarly, no small fox has been identified in mainland assemblages.

Bayesian phylogenetic analysis in BEAST (Drummond and Rambaut 2007) of all unique mainland and island haplotypes (Figure 3.3) used the earliest island fox radiocarbon date as a prior estimate for the coalescence of all island fox lineages. This tree yielded the same topology as a maximum likelihood analysis with *Vulpes* and *Canis* outgroups; both trees had strong support (Appendix A, Figure S2). Our phylogenetic analysis (Figure 3.3) revealed that fox haplotypes fell in two well-supported and divergent clades (Clades A & B). However, gray foxes from southern and northern California did not show a strong pattern of contemporary phylogeographic structure, and their haplotypes did not form reciprocally monophyletic clades. Haplotypes in clade A included all individuals sampled in southern California, plus some haplotypes from northern California. Our estimates of divergence suggest that clades A and B diverged approximately 22,900 years ago (95% Highest Posterior Density [HPD]: 35,300-13,500). Remarkably, island fox haplotypes formed a monophyletic clade nested within clade B, rather than with foxes from southern California, closest to the Channel Islands. Among the gray foxes sampled, the haplotypes that were more closely related to the island fox were from Lassen/Shasta counties in northern California. Our estimates suggest that gray and island foxes diverged ~9200 years ago (95% HPD: 13,300-6100) and that the divergence between foxes on the northern and southern islands likely occurred ~7100

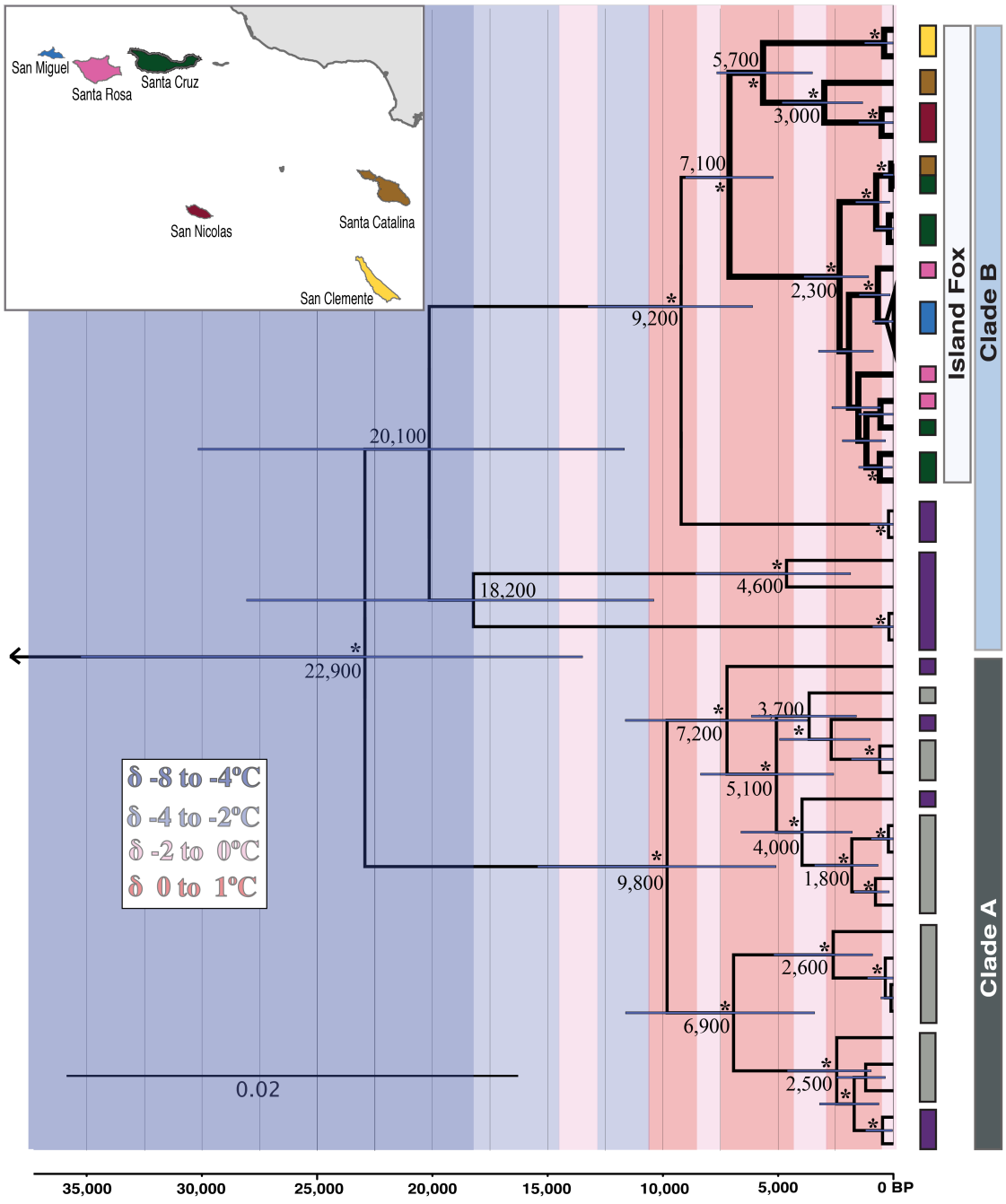


Figure 3.3 Bayesian phylogeny of mitogenomes of island and mainland foxes. The northern Channel Island foxes (San Miguel, Santa Rosa and Santa Cruz) diverged from the southern island foxes (Santa Catalina, San Clemente, and San Nicolas) ~7100 years BP (lineage bolded). Northern California (purple) and southern California (gray) foxes show patterns of climate-induced expansion. Divergence dates were calculated in BEAST v1.7.5 with node bars indicating height 95% highest posterior density. Nodes with * indicate greater than 0.99 posterior probability. Global surface temperature is overlaid in δ °C to show how climatic events may have impacted fox diversity (Tausch et al. 2006; West et al. 2007; Woolfenden 1996). Local temperature curves were not used due to the geographic distance sampled and the short time scale of local curves.

years ago (95% HPD: 9000-5200). Collectively, the radiocarbon, archaeological, paleontological, and genetic evidence roughly support the ~9200 and ~7100 estimates. Note that central California is our weakest sampling area. Future studies should focus on obtaining samples in this region.

Discussion

Gray and Island Fox Phylogeography

A broad scale analysis of the evolutionary relationships of *Urocyon* lineages should be conducted because in this study, we found that eastern and western gray fox populations are more deeply diverged than the two currently recognized species of California *Urocyon* (Appendix A, Figure S2). Furthermore, the island fox mitogenomic diversity (Figure 3.3) is nested within that of the northern California mainland gray foxes. Adaptive divergence between island and mainland populations is likely and nuclear data will be important for re-examining species and sub-specific designations.

We propose the following hypothesis for the phylogeographic pattern observed in clade A California mainland gray foxes: During the late Pleistocene, approximately 23,000 years ago (Figure 3.3) populations of California foxes diverged into two well-supported clades (clade A and B). Glacial climatic fluctuations caused habitat changes, including the appearance of continental ice sheets as far south as Washington State (Booth et al. 2003), that may have caused range shifts in locally adapted gray fox populations, with foxes with clade B haplotypes existing as far south as southern California. The current northern range extension of gray foxes is well into northern Oregon. However, the climate-induced shifts in habitat that occurred during the late Pleistocene, may have influenced a southward shift in the distributional range of gray

foxes. As the climate warmed during the Holocene, and suitable habitat expanded northward, gray fox population ranges shifted further north resulting in foxes with clade A haplotypes distributed as far north as Shasta County in northern California (Figure 1). Niche modeling with finer-scaled sampling and further genetic analysis is needed to test our hypothesis. Interestingly, a similar climatic-induced, phylogeographic pattern was found in eastern gray foxes (Bozarth et al. 2011). The historic expansion of gray foxes into northeastern US during the Medieval Climate Anomaly may have coincided with the expansion of eastern deciduous forests (Bozarth et al. 2011).

Island foxes form a monophyletic group within the northern California gray fox clade (Clade B; Figure 3.3). Santa Catalina and Santa Cruz foxes share a haplotype (Figure 2), suggesting a recent human introduction of foxes from Santa Cruz to Catalina. This scenario is supported by similarities between these islands in morphological and mtDNA restriction hybridization data collected before 1990 and the later fox population bottlenecks (Collins 1993; Wayne et al. 1991). Santa Catalina was a center for trade between Native Americans on the mainland and the southern and northern Channel Islands, with evidence for exchange of a variety of goods including soapstone artifacts from Santa Catalina quarries (Collins 1993; Rick et al. 2005).

Previous analyses using mtDNA RFLP's identified more mtDNA haplotypes than detected by our whole mitogenome (WMG) sequencing analysis on San Miguel (2 RFLP: 1 WMG genotypes) and Santa Catalina (3 RFLP: 2 WMG genotypes), suggesting a possible loss of mtDNA diversity on these islands as a result of population bottlenecks over the past 25 years (Wayne et al. 1991). MtDNA RFLP data from Santa Cruz, Santa Rosa, San Nicolas, and San Clemente identified the same number or one fewer

haplotypes than whole mitogenomes. Sample size does not account for this pattern as mitogenome sample sizes were larger on all islands except Santa Rosa and San Nicolas. San Nicolas island foxes were found to be monomorphic at 18 microsatellite loci but showed higher heterozygosity in MHC loci (Aguilar et al. 2004). We identified two pairs of closely related haplotypes on each of the two most remote islands in the archipelago (San Nicolas and San Clemente), which indicates *in situ* evolution of island fox genetic variation. Furthermore, the fox populations on San Nicolas and San Clemente islands did not undergo as severe population crashes as the other island fox populations experienced. This might explain the presence of additional haplotypes, especially in comparison to the population crashes and the potential loss of genetic diversity on San Miguel and Santa Catalina.

We find evidence of discrete island-specific matrilines and microsatellite loci detected a strong signal of population genetic structure in island foxes (Goldstein et al. 1999). Mitogenomes can recover patterns at greater time depths than microsatellites, which are likely to reflect recent and dramatic changes in nuclear allelic frequencies caused by genetic drift (Aguilar et al. 2004; Goldstein et al. 1999). Strong population differentiation among microsatellites can occur in just decades (Munshi-South and Kharchenko 2010), so it is plausible to detect both fine-scale genetic structure with microsatellites and low levels of divergence between mitochondrial lineages.

Origins of the Island Fox

The diversification events influencing island and mainland gray foxes closely correspond to climatic fluctuations, particularly the shift from fully glacial to non-glacial conditions during the past 20,000 years. The arrival of foxes on the Channel Islands could

have occurred when the range of clade B gray foxes shifted into southern California. Our divergence date estimates for the island fox clade itself, ~9200 years ago, as Santarosae separated into four distinct islands and for the southern island fox lineage, ~7100 years ago, correspond well with the earliest AMS dated island fox bones (~7100 cal BP for northern and ~5640 cal BP for the southern islands). All of these data imply a Holocene colonization. However, the fact that we detected only 13-14 base pair substitutions between the closest mainland gray fox lineage and the northern/southern island fox ancestor suggests that the date of divergence for the island fox clade could be more recent than 9200 years ago.

Radiocarbon dates of nine island fox bones suggest that the northern Channel Islands were colonized first, followed by dispersal to the southern islands. Island foxes show greater mitogenome diversity in the northern islands with nine haplotypes that differ from 2-5 base pairs from the central node of the star-shaped radiation (Figure 3.2). This pattern is strikingly different from the southern islands, where San Clemente and San Nicolas each have two haplotypes just a single base pair away from each other. The greater genetic diversity and radial haplotype pattern in the northern islands may have taken longer to occur than the single mutational step found in the southern islands. However, a bottleneck in the northern islands followed by population growth could also generate this pattern. The mitogenomic data are consistent with the archaeological evidence that supports the hypothesis that foxes dispersed from northern to southern islands but more data are needed to confirm a northern to southern island dispersal.

Island foxes are not strong overwater dispersers and it is extremely unlikely they reached the more remote southern islands without human intervention (Collins 1991a,b;

Wenner and Johnson 1980). Therefore, the substantial divergence between southern and northern island lineages in network and phylogenetic analyses implies that foxes were moved to the southern islands soon after they arrived on the northern islands. Our results suggest that southern island lineages diverged from each other 5470-5640 cal BP to 5700 years ago (95% HPD: 7700-3500) based on radiocarbon and genetic date estimates, respectively. Although the estimates obtained by radiocarbon dating may more accurately represent the arrival date rather than a divergence date estimate provided by the mitogenomic data, the radiocarbon dates and divergence estimates are very similar. Previous estimates using microsatellites and an ultrametric UPGMA bootstrap consensus tree based on $(\delta\mu)^2$ genetic distances with low support calculated the divergence of southern lineages (excluding San Nicolas) to be 5539 years ago and 12,000 years ago for the island fox lineage as a whole (Goldstein et al. 1999). These earlier estimates were calibrated using a presumed initial fox introduction date of 16,000 years ago, which is no longer supported by AMS radiocarbon dates or other evidence.

Our genetic results also indicate that divergence within northern island lineages occurred more recently than our radiocarbon dates. The divergence estimate of 2300 years ago for all northern island lineages may be evidence of a severe bottleneck that either happened before 2300 years ago and resulted in the reduction of ancient mtDNA lineages, or an indication that northern island fox populations were panmictic due to human intervention before 2300 years ago. Estimates of divergence using microsatellites between San Miguel and Santa Rosa, yielded a date of 2079 years ago, which is comparable to our results (Goldstein et al. 1999). Although in the same analysis, the Santa Cruz lineage shows a deeper divergence (7522 years ago), which is very close to

our estimates of the entire island fox lineage. However, this node in the microsatellite analysis is not well supported with a bootstrap value of 49.6%. Interestingly, the most recent 3500 years of prehistory was a time of Native American population growth and sociopolitical changes, perhaps increased human-induced fire, as well as a period of climatic instability (Anderson et al. 2010; Kennett 2005), both of which could have affected contemporary levels of mtDNA diversity. Present day population dynamics and climatic events may have similar effects as past climate instability.

The precise mode of fox colonization of the northern islands remains unclear, but our genetic and radiocarbon data indicate that this event occurred well after human colonization (~13,000 cal BP). Two hypotheses provide plausible colonization scenarios. First, a single pregnant fox or even a few closely related foxes, rafted to the northern islands while Santarosae was splitting into four separate islands (or just after they had separated) between 10,000-9000 cal BP or later. Gene flow between the islands decreased and populations became isolated, giving rise to island-specific lineages. Humans later transported island foxes to San Clemente, Catalina, and San Nicolas islands. The second hypothesis is that Native Americans introduced foxes coincident with the breakup of Santarosae. Similar to the first hypothesis, island foxes were then moved to the southern islands. We cannot reject either hypothesis, but both involve prehistoric human intervention and translocation. The ancient gray fox lineage that gave rise to all island foxes appears to be unsampled and may be rare or extinct in the extant gray fox populations. Ancient DNA analysis of archeological samples are needed to further distinguish between these different scenarios, because prehistoric and recent bottlenecks may confound the patterns that we obtained from contemporary fox samples.

Endemism and Rapid Evolution

Our data suggest that the rapid evolution of unique behavioral and morphological features associated with island endemism in *U. littoralis* is the result of close interaction with humans as well as island evolutionary pressures and climate change. The small size and tameness of island foxes are traits often linked to insular evolutionary pressures (Foster 1964). Island fox dwarfism may have occurred rapidly (2 millennia or less) because the earliest fox bones (~7100 cal BP) were already small in size. Alternatively, island foxes may have originated from small mainland gray foxes, but we have no evidence that such a mainland population existed. Island dwarfism is thought to result from intense natural selection caused by evolutionary pressures of living on islands (e.g., increased competition for limited resources) (Raia and Meiri 2006). Rapid morphological change has occurred many times in mammalian evolutionary history (Cuarón et al. 2004), with and without human intervention, including domestic dogs (Boyko et al. 2010) and silver foxes (tamed from wild Russian red foxes (*Vulpes vulpes*) (Kukekova et al. 2008, 2011; Lindberg et al. 2005).

We detected limited evidence for natural or artificial selection in island fox mitogenomes. A comparison of mitogenomes from 16 pairs of domestic animals and their wild progenitors revealed no consistent patterns between divergence date, dN/dS, and branch length (Moray et al. 2014), indicating that human-mediated selective pressures did not have consistent mitogenomic effects. Changes to dn/ds in some of these domestic/wild animal comparisons may be the result of reductions in effective population size leading to relaxation in selective forces. However, the average difference between dN/dS was only 0.0342 in these domesticated/wild comparisons (Moray et al. 2014),

whereas island foxes (0.40) have almost a fourfold greater dN/dS ratio than California mainland foxes (0.10). This elevated dN/dS ratio in island foxes may be due to reduced effective population size during colonization, bottlenecks, or artificial selection.

Humans have had close associations with island foxes for thousands of years, which could have exerted selective pressure for a small, tame fox phenotype, Native Americans practiced intentional island fox burials (Collins 1991a: 199,b) and translocated island foxes to the southern islands early in the evolutionary history of *U. littoralis*. Anglo-American ranchers purportedly introduced a few island foxes from Santa Catalina to San Clemente in 1875 (Johnson 1975) and island foxes were kept as pets in the 20th century (Collins 1991a; Johnson 1975). Clearly, island fox evolutionary history has been intertwined with humans across the entire timespan of Native American, Euro-American ranching, and modern conservation management eras.

Island-specific mitochondrial lineages and *in situ* evolution also suggest that island foxes have undergone dramatic and rapid evolution over the past ~9-7000 years. Despite small population sizes and limited geographic distribution, island foxes have generated and maintained mitochondrial diversity, even with population reductions to only 15 individuals on some islands during the 1990s (Coonan et al. 2010). These island fox data, however, do not reveal the past diversity that may have been lost during recent or even historical bottlenecks (Campos et al. 2010a; Hoelzel et al. 2002b). Regardless of whether the original fox population arrived on the Channel Islands by natural or human dispersal, island foxes have adapted to and weathered dramatic environmental and cultural change for more than seven millennia.

This study provides a new approach to integrating archaeological, paleontological, and biological datasets to examine biogeographic patterns of wild animals and plants and the evolution of endemic and endangered species. Collaborative research teams of archaeologists, biologists, geneticists, and resource managers can generate new insights about the evolutionary histories of other endemic taxa. We expect such investigations of the deep histories of human-animal interactions to become increasingly important for understanding the relationships between people and the natural world and for guiding conservation decisions.

Materials and Methods

AMS Radiocarbon Dating

All ages derived from AMS radiocarbon dates are in calibrated calendar years (cal BP) unless otherwise noted (Appendix A, Text S1 and Table S3).

Mitogenome Sequencing

For this study we exclusively used tissue samples that had previously been deposited in several frozen tissue collections from recognized institutions including those housed at CCEG, at the Smithsonian Conservation Biology Institute, the Santa Barbara Museum of Natural History, the Catalina Island Conservancy, the Museum of Vertebrate Zoology at Berkley, the Colorado State University, the Nature Conservancy, the National Park Service collections (permit number CHIS-2012-SCI-0006) including the National Park Service Special Collection at Ambrose Monell Cryo Collection at the American Museum of Natural History (see Appendix A, Table S1). No animals were trapped or sacrificed for the purposes of this study and therefore, a formal approval by an

Institutional Animal Care and Use Committee was not necessary. Total genomic DNA was extracted in a PCR product-free extraction lab using DNeasy Blood and Tissue DNA kits (Qiagen). 185 whole mitogenomes were generated from 201 samples using three different library prep protocols and two sequencing methods, 454 and Illumina (Appendix A and Appendix A, Table S1). The same haplotypes were recovered from both sequencing methods indicating no sequencing method bias.

Raw reads were trimmed, filtered and mapped with BWA v.0.7.4 to a gray fox reference that was assembled deNovo with Mira v3.4.0. Consensus sequences and coverage were calculated with SamTools v0.1.19 and all consensus sequences were aligned with Mafft v7.017. The aligned mitogenomes were visually examined and when a single island individual or an ambiguous base generated a unique haplotype, Sanger sequencing was conducted to verify the basecalls (Appendix A and Appendix A, Table S4), which did not change except for two samples with conflicting haplotypes that was discarded from all analyses. Sequences have been deposited in GenBank (accession numbers KP128924- KP129108).

Summary analyses were completed in DNAsp v5.10.1, GenALEx v.6.5 and Arelquin v3.5. Network analysis was conducted on an alignment stripped of monomorphic sites using the median joining algorithm and default parameters of Network v.4.612. Selection analysis was completed using an alignment of coding genes (11,286 bp), and a neighbor-joining tree with the same topology as the Bayesian and ML tree. These datasets were uploaded to the HyPhy data server and six algorithms were used with the HKY85 model.

Phylogenetic Analyses

To examine phylogenetic relationships between island, California and eastern gray foxes, additional publically available mammal mitogenomes were obtained from GenBank and aligned to the fox dataset. The alignment was run through JModelTest v.2.1 and the GTR+I+ Γ model was used to run 1000 pseudobootstrap replicates of the maximum likelihood tree program Garli as implemented on the Lattice grid computing system (Bazinet et al. 2007; Zwickl 2006).

To date the divergence between island and mainland foxes, Bayesian phylogenetic analysis was conducted in BEAST v.1.7.5. Each gene, as well as the entire alignment, were run through JModelTest v2.1 and PartitionFinder v1.1.1. Based on this analysis, no codon partitioning and empirical base frequencies were used with each gene fitting the HKY or the TN93 model. Both a lognormal relaxed and strict clock were tested with a coalescent of constant size. The earliest calibrated radiocarbon date was used as a prior estimate of the time to the most recent common ancestor for all island fox samples. An eastern gray fox sample was used as an outgroup as indicated by the maximum likelihood analysis. The eastern gray fox is deeply diverged from California foxes but this split must be younger than the oldest fossil date for *Urocyon* so we set the root length to the early Pliocene *Urocyon* fossil dating to 5.332-2.558 MYA (McKenna and Bell 1997).

All other priors were left to default settings and the MCMC was run in two independent runs of 100 million chains each, logging every 10,000 chains. An empty alignment was tested to sample for effects of the prior and the resulting poor posterior and prior ESS with values below 200 indicated that the priors were not strongly

influencing the tree. Substitution rates were compared to other canids and mammals (see Appendix A) to examine how the radiocarbon date prior influenced divergence dates.

Chapter 4: Tracking the diet of an endangered carnivore across 7300 years of human cultural and environmental change

Introduction

Humans have had a significant influence on past and present wildlife population demographics, genetic diversity, and biogeography (Grayson 2001; Lorenzen et al. 2011; Rick and Erlandson 2008a; Storey et al. 2013; Zeder 2015), and a growing body of evidence demonstrates that people have also impacted the foraging ecology of wild animals (Auman et al. 2011; Bentzen et al. 2014; Kristan et al. 2004; Merkle et al. 2011; Newsome et al. 2010; Wiley et al. 2013). Landscape clearance, burning, or introducing different flora and fauna can alter local resource availability for native animal taxa. The effects of these changes can be particularly challenging for endangered animals or those with small population size as even minor perturbations can impact habitat quality and by extension resource availability. Understanding these anthropogenic changes to wildlife foraging patterns is important as we plan for future climate change and mitigate the effects of habitat alteration, both of which can have implications for wildlife management.

Wildlife diets can be altered through intentional or unintentional provisioning by humans or due to anthropogenic changes to ecosystems and resource availability. Urban wildlife is particularly susceptible to changes in diet associated with scavenging from human refuse (Auman et al. 2011; Kristan et al. 2004; Newsome et al. 2010, 2015). Dietary changes have also been identified in animals under captive management (Sugiyama 2014) and during domestication by ancient peoples (Axelsson et al. 2013;

Barton et al. 2009; Fuller et al. 2012; Hu et al. 2008; White et al. 2001). Human provisioning of animals is an important step in the domestication process (Makarewicz and Tuross 2012; Zeder 2006a,b) and evidence of human provisioning may indicate the initiation or an ongoing domestication relationship. Unintentional or intentional human provisioning of wild animals can also impact body condition (Heiss et al. 2009) and the ability of an animal to teach their young how to forage outside of human refuse. With such profound changes to wildlife diet from human activities, long-term datasets are valuable for identifying anthropogenic impacts and documenting ecosystem change and variability that could be important in managing wildlife populations for future change.

Stable isotope ecology is an important tool for exploring anthropogenic impacts on wildlife foraging, providing insight into past and present human-wildlife interactions. To examine temporal changes in foraging patterns and to explore the use of stable isotopes to evaluate resource provisioning in human-wildlife relationships, we focus on the chronology and isotope ecology of the endangered Channel Islands fox (*Urocyon littoralis*). The endemic island fox is found on six of the largest Channel Islands (Figure 1). It is a small relative of the gray fox (*Urocyon cinereoargenteus*) that occurs on the adjacent California mainland. Several AMS radiocarbon dates suggest that the island fox may be a recent arrival to the islands. The oldest published island fox remains on the islands are found in archaeological sites and date to ~7100 years ago (Hofman et al. 2015; Rick et al. 2009b; Vellanoweth 1998) long after humans first colonized the islands at ~13,000 cal BP (Erlandson et al. 2011). Mitochondrial genomes also support an early to mid-Holocene introduction (Hofman et al. 2015). It is unknown how foxes first arrived on the Channel Islands, with hypotheses ranging from a human introduction to a natural

rafting event or a combination of the two (Aguilar et al. 2004; Collins 1991a,b, 1993; Hofman et al. 2015; Johnson 1975; Orr 1968; Rick et al. 2009b; Vellanoweth 1998; Wayne et al. 1991). Evidence of resource provisioning by humans could lend support to a human introduction and suggest a relationship of semi-domestication by humans.

Here we review and analyze the human-fox relationship by examining carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values in bone collagen from paleontological, archaeological, historic, and modern island fox samples. We also resolve the island fox chronology by synthesizing 27 new and previously reported AMS ^{14}C dates measured directly from archaeological island fox samples. Together these data address three interrelated questions: How do ancient and modern island fox diets compare? Did ancient humans influence island fox foraging behavior? Were island fox diets affected by changes in human occupation (Native American, historical ranching, conservation) or climate changes? Investigations of human impacts on island fox foraging behavior can also help expand our understanding of the evolutionary history of ancient human impacts on and future management of this endemic island carnivore.

Background and Context

Stable Isotopes and the Canine Surrogacy Approach

To investigate changes in the diet of island foxes, we adopt a "Canine Surrogacy Approach" (CSA), which has been used to investigate human provisioning of dogs in the archeological record and dietary changes in humans (Cannon et al. 1999; Guiry 2012; Rick et al. 2011a; Tankersley and Koster 2009). CSA assumes that dogs are eating similar foods as their human handlers (handouts and scavenging) and thus dog isotope data reflect those of human diets. Therefore, dogs can be used as a proxy for human diet

in the archaeological record when human bone samples are unavailable or sampling is prohibited (Guiry 2012). While dogs have been good proxies for humans, isotope values from canid bone collagen likely reflect the average of shorter periods of time than humans due to differences in bone turnover rates and shorter lifespans (Guiry 2012; Pearce et al. 2007). Weaning effects can also impact isotope values as juveniles and pups have increased $d^{15}N$ and may not be identified in the archaeological record (Guiry 2012). However, the use of canids remains a valuable method for testing for human provisioning in wild animals, like the island fox.

On the Channel Islands, a small sample of (n=3) late Holocene island foxes recovered from an archaeological site on Santa Rosa Island (CA-SRI-2), show different $\delta^{13}C$ and $\delta^{5}N$ values than humans and dogs from the same site (Rick et al. 2011a). These isotope values likely reflect the consumption of rodents, insects and plants, similar to that consumed by modern foxes (Cypher et al. 2014). While there is continuity between the diet of late Holocene fox diets and modern foxes on Santa Rosa, the sample is small and questions remain about fox diet across space and through time. Here we expand on these preliminary data and evaluate potential for human provisioning of foxes drawing on a large dataset (n>200) of island foxes spanning 7300 years and seven islands. If there is considerable human-fox interaction in a commensal or mutually beneficially relationship, foxes might be eating scraps and human refuse, which can be tested by comparing dietary isotopic signatures between the humans, dogs and foxes. If humans and foxes interacted more closely following the arrival of foxes on the islands, we might expect similar isotope values to humans in early foxes. This could support a human introduction of

foxes to the Channel Islands but more data would be needed to support a definitive human introduction.

Alternatively, if foxes were scavenging marine carrion including pinniped carcasses we also might expect enriched nitrogen and carbon. However, occasional scavenging of marine resources might not be detected in bone collagen because bone collagen is a dietary average spanning at least several months. Thus foxes enriched in carbon and nitrogen were likely consistently consuming resources at a high trophic level. Distinguishing between human resource provisioning and scavenging of marine carrion is difficult so for the purpose of this study, we are considering human provisioning as the consumption of resources within the 95% confidence ellipses of human populations from the Channel Islands. These isotope values in bone collagen would require considerable and consistent consumption of marine resources which have not been detected in modern fox populations (Cypher et al. 2014). Island foxes may also have been valued for their role in managing island mice populations. If this were the case we would expect a diet consistent with lower trophic, terrestrial foods. Comparisons between archaeological and modern stable isotope bone collagen data can also help us explore human resource provisioning and long-term trends in island fox diet.

The California Channel Islands and Island Foxes: What do we know?

The Channel Islands are a series of eight islands on the coast of California, ranging from 20 to 98 km from the mainland. While the Channel Islands have never been connected to the mainland during the Quaternary, the northern islands (San Miguel, Santa Rosa, Santa Cruz and Anacapa) were connected to each other as a single landmass (Santarosae) in the Pleistocene, which began to separate around 11,000 cal BP and was

completely separated by 9000 cal BP (Figure 4.1) (Muhs et al. 2012, 2014; Reeder-Myers et al. 2015; Wenner and Johnson 1980). The southern islands were larger when sea levels were lower but were not connected to each other or the mainland. The paleogeography of the islands also has significantly affected island biodiversity (Johnson 1983, 1975, 1980; Wenner and Johnson 1980). Surrounded by extensive and productive marine ecosystems, Channel Island terrestrial landscapes are less diverse with only five extant endemic

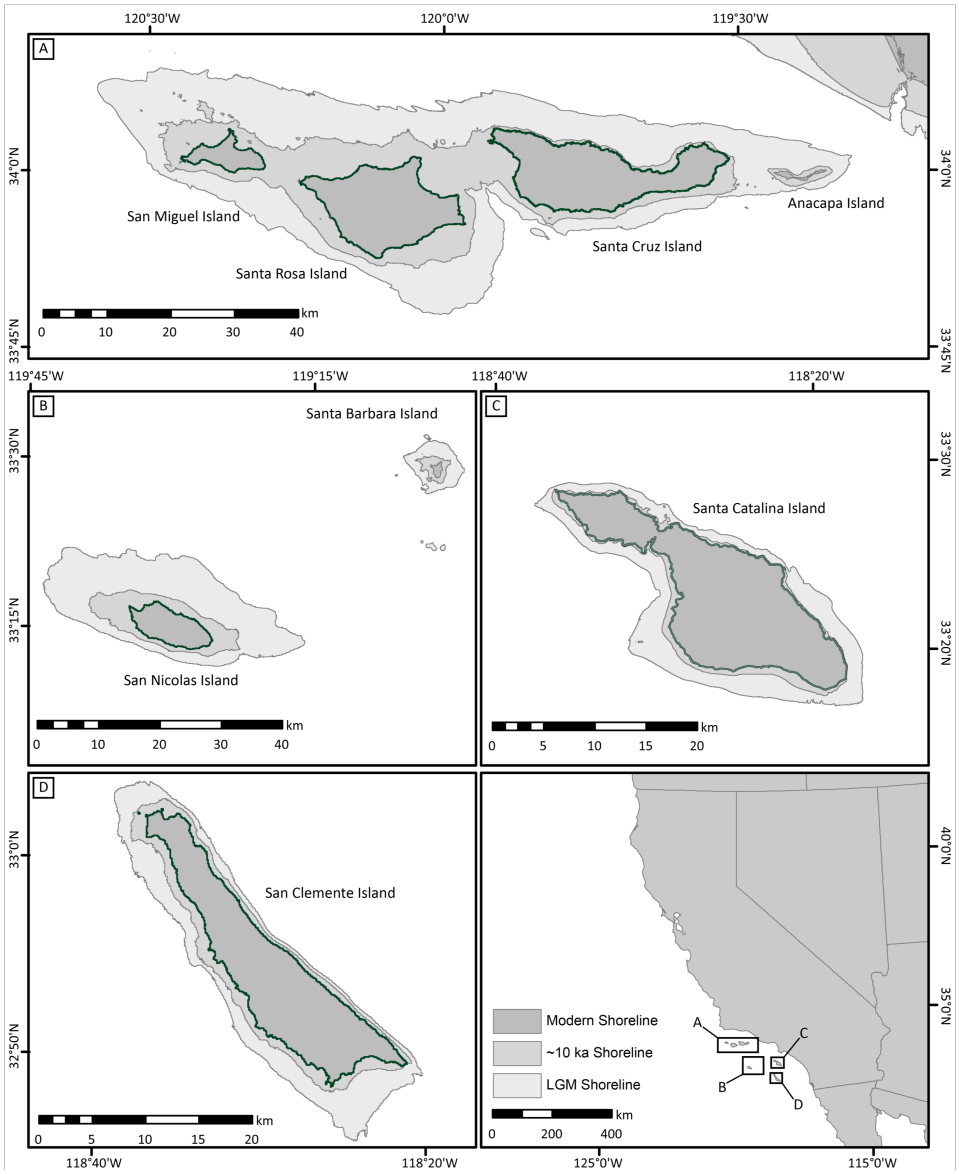


Figure 4.1 Map of the California Channel Islands. Island shape and size are modeled at key time points (Last Glacial Maximum, 10,000 cal BP, and present day). Islands with extant island fox populations are outlined in green.

terrestrial mammals: the island fox, Catalina ground squirrel (*Spermophilus beecheyi nesioticus*), the island spotted skunk (*Spilogale gracilis amphiala*), the deer mouse (*Peromyscus maniculatus*), and the ornate shrew (*Sorex ornatus)*, with each of these animals unevenly distributed on the islands (Rick 2013). Native Americans also introduced dogs to many of the islands during the middle Holocene (Rick et al. 2008) and a number of non-native and invasive species arrived in the last 200 years.

From ancient hunter-gatherers, to historic ranchers, island landscapes have changed dramatically since people first arrived on the islands 13,000 years ago (Rick et al. 2014). During the warmer drier transition at the terminal Pleistocene, the islands shifted from temperate forests to shrublands/grassland and by 11,000 cal BP coastal sage shrub dominated the landscape. Pollen and charcoal from Santa Rosa Island suggest that by 6900 years ago grassland and perennial herbs predominated and the evidence of wetland plants suggests that the region became wetter around 4500 years ago (Anderson et al. 2010; Rick et al. 2014). Fire frequency also increased around 9150 years ago and again 3500 years ago (Anderson et al. 2010) with the latter thought to be from burning by Native Americans. During the ranching era (mid 1800s-late 1900s), introduced livestock (sheep, goats, cattle, horses, donkeys, pigs) and game species (bison, elk, deer, and turkey) transformed the landscape due to overgrazing and trampling of the native grassland that caused vegetation changes and large-scale erosion (Johnson 1980; Rick et al. 2014). Most of the game species and livestock have been removed from the islands and vegetation communities are recovering (Corry and McEachern 2009). Today, the islands are managed for conservation, recreation, and defense by the National Park Service (NPS), the Nature Conservancy, the Navy, and the Catalina Island Conservancy,

with active research and conservation activities conducted by a wide variety of universities and agencies.

As one of the only terrestrial mammals on Channel Islands, the island fox is an apex predator and currently of considerable conservation concern. In the 1990s, fox numbers dropped rapidly due to introduction of distemper by domestic dogs and by golden eagle predation (Coonan et al. 2010). In response, NPS removed and relocated the golden eagles that had recently colonized the islands from the mainland and bald eagles were reintroduced. With the threat of extinction, the Island Fox Conservation Working Group conducted a ten-year captive breeding program on Santa Rosa, San Miguel, Santa Cruz, and Santa Catalina. The last captive fox was released in 2008 and island fox numbers have increased considerably (Coonan 2013; Coonan et al. 2010, 2014). Ongoing island restoration activities have focused on increasing fox populations and restoring landscapes to their pre-ranching state.

Today, island foxes are opportunistic omnivores with seasonal and spatial variation in diet. Beetles, deer mice, (*Peromyscus maniculatus)*, lizards, jerusalem crickets (*Stenopalmatus spp.*), and other insects, terrestrial snails, and number of a native and non-native fruits were important resources identified in island fox scat (Cypher et al. 2014). Additionally, island foxes ate birds year-round and scavenged introduced ungulates where available, especially in the fall and winter when hunters leave "gut piles" during dressing (Cypher et al. 2014). When herd animals were present on the islands, foxes also scavenged livestock carrion (Laughrin 1977). Cypher et al. (2014) found trace amounts of pinnipeds (less than 5 occurrences in a season) in island fox scat from San

Nicolas, San Miguel, San Clemente, and Santa Catalina suggesting minimal marine dietary input.

While there has been considerable research on the island fox, the origin of the island fox is still unclear. The island fox's reduced size relative to mainland gray foxes suggests that the fox has been on the islands for a significant time. Despite claims of fossil foxes as old as 40,000 or 16,000 years old and prior to human arrival (Collins 1991a; Guthrie 1993; Orr 1968), direct AMS dating and re-analysis of these specimens demonstrated that foxes appear on the islands around ~7100 cal BP (about the same time dogs appear in the archaeological record) (Hofman et al. 2015; Rick et al. 2008, 2009b). There is also no archaeological or paleontological evidence of island fox ancestors such as a small grey fox. Rapid morphological change is possible and can occur in very short time periods (Cuarón et al. 2004; Gompper et al. 2006), but there is little evidence of morphological change through time within the island fox (Collins 1991a,b, 1993). Native Americans likely deliberately introduced foxes from the northern Channel Islands to the southern Channel Islands at least 5,000 years ago (Hofman et al. 2015), and a growing body of evidence suggests that Native Americans may also have first introduced foxes from the mainland (Rick et al. 2009b). This is supported by their widespread distribution on the islands, their absence in fossil deposits or in very early archaeological contexts, significance of foxes in Native American religion and ceremony (including over 51 fox burials) and use of fox pelts, changes in ground nesting birds in fossil deposits following hypothesized early Holocene fox colonization, as well as evidence for rapid dwarfing among mammals (Collins 1991b; Rick et al. 2009b). While there is little evidence of human consumption of island foxes (Collins 1991b), island foxes bones have

been recovered in a variety of archaeological contexts including middens, intentional burials, and associated with human cemeteries indicating a diverse set of human-fox interactions (Collins 1991a,b; Hofman et al. 2015; Vellanoweth 1998). However, significant questions remain about the how ancient peoples and dramatic landscape change during the Holocene impacted island fox populations.

Materials and Methods

Specimens

Paleontological, archaeological, historical and recent island and recent gray fox bones were obtained from the collections at Santa Barbara Museum of Natural History, United States National Museum, Cal State-LA, Cal State-Northridge, and Catalina Island Museum (Appendix B, Table S1). Archaeological island fox (n=64) samples come from 25 different archaeological or subfossil localities, or more than 47 percent of the sites where foxes have been identified (n=53). In selecting archaeological samples, we surveyed published and unpublished accounts of island and gray foxes, investigated museum collections, and contacted colleagues to ensure that we had the widest temporal and spatial coverage possible. Our goals were to make sure that we had samples from the potential oldest foxes on each island and had good diachronic coverage. Island foxes from the late ninetieth (n=34) and island (n= 118) and gray foxes (n=24) from the twentieth century fill in more recent time gaps. Although intentional fox burials have been recovered on the southern and northern islands (see Collins 1991b), the vast majority of archaeological specimens represent a single bone or small number of bones from unknown or poorly documented contexts, making associations problematic for

helping understand fox diet and relationships with humans. We were able to sample a number of these possible fox burials (n= 25) but not all burials were available for study.

To sample for isotope and AMS dating a small (ca. 500-1000 mg) fragment of island fox bone was removed using a clean blade, tweezers, or a new dremel head. When crania were present, bone was sampled from nasal turbinates or the tentorium plate inside the cranium. In some cases, only long bone fragments were available and were cut with a dremel tool while taking advantage of broken areas. For archaeological specimens, we sampled different excavation units and, when possible, the same element and side to minimize the possibility of sampling the same individual.

AMS Radiocarbon Dating

Previous studies have reported eight AMS radiocarbon dates on island fox bones (Hofman et al. 2015; Rick et al. 2009b; Shelley 2001). To expand on these data, AMS radiocarbon dates were obtained for 19 island fox bones with the aim of documenting the antiquity and evolution of island foxes. Samples were chosen to represent some of the potential oldest island fox remains or sites with long occupational histories and complex stratigraphy. These include specimens from the following sites, SCAI-17, SRI-1, -3, and -5, SCRI-333, and SMI-1 and -261, that have trans-Holocene deposits and fox remains came from the surface or unknown contexts (see Table 4.1).

Bone fragments were sent to the Oxford Radiocarbon Accelerator Unit (ORAU) at the University of Oxford. The bones were pretreated using ultrafiltration techniques and collagen was extracted and analyzed for the ^{14}C (Ramsey et al. 2007a,b). All dates were calibrated using OxCal v. 4.2 (Ramsey 2009, 2013). Because some foxes may have been consuming high amounts of marine resources, which would require a marine reservoir

correction (**Δ**R), the ORAU measured the ^{13}C values for each specimen independently from the radiocarbon analysis. None of the specimens required a **Δ**R correction. A previously reported date from SNI-11 without a $\delta^{13}C$ value was corrected (261±21; (Jazwa et al. 2012) due to evidence of marine diet in archaeological foxes on San Nicolas. All dates were calibrated using the Intcal13 except for the fox from SNI-11 which used the Marine13 calibration dataset (Reimer 2013).

Stable Isotope Analysis

For $\delta^{13}C$ and $\delta^{15}N$ analysis, dog (n=1), gray fox (n=24), and island fox (n=204) bone fragments were demineralized in 0.5 N hydrochloric acid (HCl) for ~12-15 hr at 5°C. The resulting material was treated repeatedly with a chloroform/methanol (2:1) mixture to remove lipids and then lyophilized. Freeze-dried sub-sample of bone collagen (~0.5 mg) were sealed in tin boats and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values were measured using a Costech elemental analyzer interfaced with a Finnegan Delta Plus gas source isotope ratio mass spectrometer at the University of Wyoming Stable Isotope Facility (Laramie, WY). Stable isotope results are expressed as δ values, $\delta^{13}C$ or $\delta^{15}N = 1000* [(R_{sample} /R_{standard})-1]$, where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. The standards are Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen. δ values are expressed as parts per thousand or per mil (‰). Fox samples from the 1860s to the present were corrected for the Suess effect following equations in (Francey et al. 1999; Wiley et al. 2013). Historic museum samples without a collection year were corrected by 0.5‰ and categorized as “Historic”. Previously reported stable isotope data from Goldberg (1993), Rick et al. (2011), and Smith (2013) were compiled for the temporal and spatial

comparison of human (n=349), dog (n=19), and fox (n=12) diets (Goldberg 1993; Rick et al. 2011a; Smith 2013). We anticipate some inter-laboratory variation in comparing these different datasets, but the majority (>94%) of the island fox data were generated in a single laboratory.

Bone collagen $\delta^{13}C$ or $\delta^{15}N$ values of humans, dogs, and foxes from archaeological, historic, and recent contexts were plotted with 95% confidence ellipses to investigate human provisioning of foxes. If a fox fell within the human 95% confidence interval, it is labeled as provisioned. Confidence intervals on a combined human/dog group did not include additional island foxes. To compare foxes between time points and island we conducted an analysis of variance as implemented in R.

Results

Island Fox Chronology

AMS dates from 19 island foxes add to published data (Hofman et al. 2015; Rick et al. 2009b; Shelley 2001) for a total of 27 directly-dated island fox bones (Table 4.1). Despite targeting potentially terminal Pleistocene and early (~11,700-7000 cal BP) and middle Holocene (~7000-3500 cal BP) contexts, we generated a largely late Holocene (3500-200 cal BP) record of island foxes on all of the islands (Figure 4.2, Appendix B, Table S2). We have identified considerable variation between known archaeological site chronologies and the AMS date of the island foxes recovered in the site. In several cases (SRI-1, SRI-3, and SRI-4), fox dates are considerably younger than the known chronology of the site (Table 4.1). The earliest evidence of the island fox comes from Cuyler Harbor on San Miguel (SMI-1) and dates to 7310-7170 cal BP and is comparable to a previously reported date from an SMI subfossil locality of V-7C. Early dates from

Santa Cruz come from the middle/late Holocene site of SCRI-333 and date to 6180-5955 cal BP. On the southern islands, the oldest fox date comes from Catalina and dates to 5640-5470 cal BP. On San Nicolas, the oldest fox dates to 5070-4790 cal BP and is contemporaneous with a fox auditory bulla from SNI-161 that has not been directly dated but has good associated radiocarbon dates (Vellanoweth 1998). The oldest fox from San Nicolas (SNI-11) could be older without a marine correction (5860-5590 cal BP). The earliest directly dated fox on San Clemente dates to 2200-2300 cal BP.

We also report the first fox documented on Anacapa Island. Island foxes are not currently present on the island nor are they known from previous archaeological or paleontological research. Five island fox bones (broken proximal left femur, matching broken distal left femur, metarsal, rib, proximal tibia), perhaps representing a single individual, were recovered from ANI-2, a shell midden on the south side of East Anacapa dated to 3250-2710 cal BP (see Jew et al. 2015; Reeder and Rick 2009 for information on ANI-2) This island fox was directly dated to 3210-3010 cal BP and fits well with the site chronology.

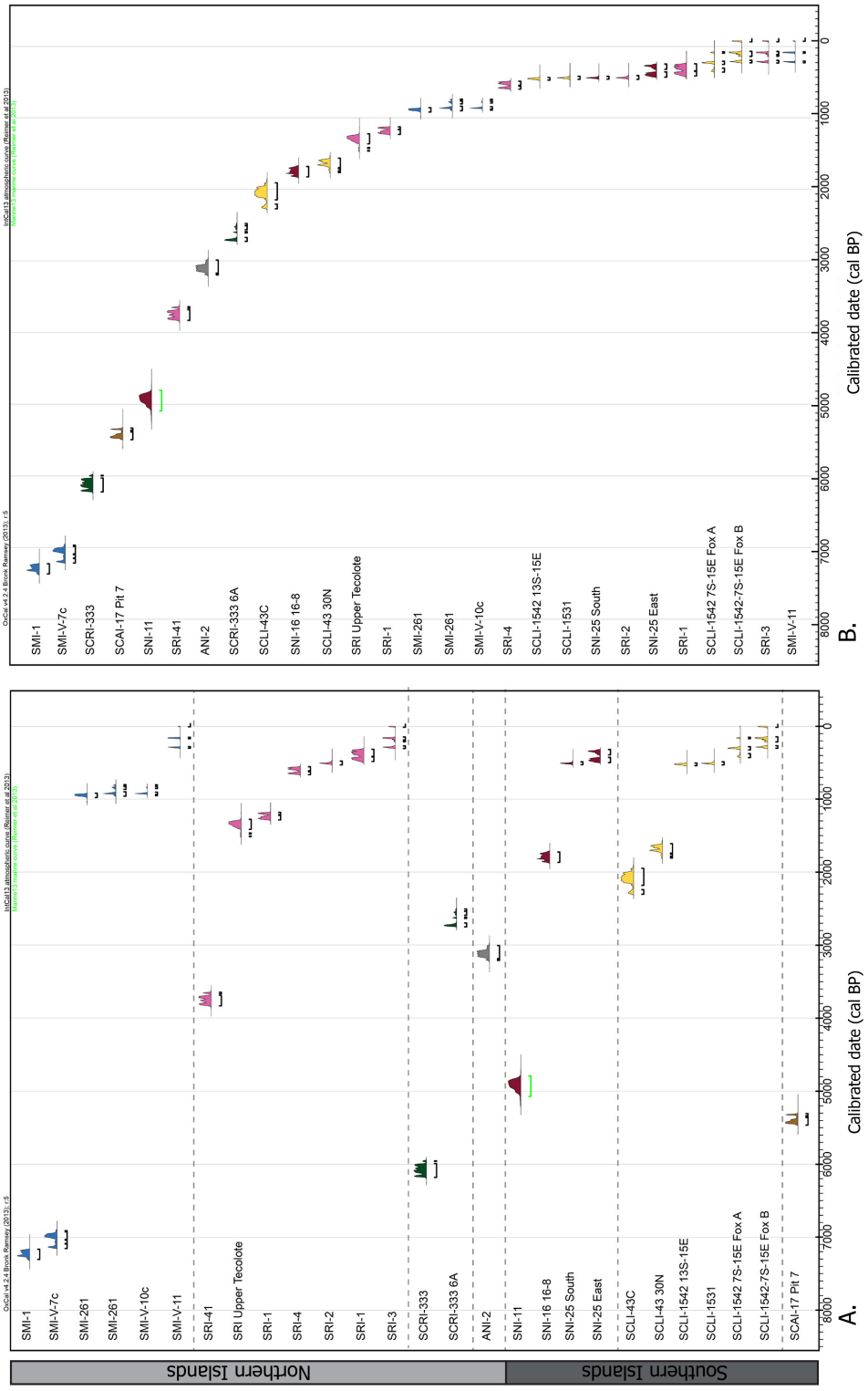


Figure 4.2 AMS Radiocarbon dates of Island Foxes. Dates are colored by island and dates with marine calibrations are highlighted in green. Radiocarbon dates are organized by island (Fig. 4.2A) and by date (Fig. 4.2B).

Table 4.1 Archaeological Samples

Island	*Site*	*Site Chronology*	*Fox Date*	*NISP*	*MNI*	*Reference*	*Isotope*
San Miguel	SMI-1	7120-3070	7310-7170	2	1	Collins (1991a); Rick et al. 2009	1
	SMI-87	4830-2360		1	1	Rick et al. 2009	
	SMI-261	12,600-550	980-920; 960-800	13	1	Collins (1991a); Rick et al. 2009	2
	SMI-470	4410-3940; 460-Historic		1	1	Rick et al. 2009	
	SMI-525	3290-470		1	1	Collins (1991a); Rick et al. 2009	-
	SMI-603	8500-910		1	1	Rick et al. 2009	1
	SMI-Locality 7C	Pleistocene	7160-6910	1	1	Guthrie (1993); Rick et. al 2009	
	SMI-Locality 10	Pleistocene	950–800	6	1	Guthrie (1993); Rick et. al. 2009	
	SMI-Locality 11	Pleistocene	300–0	1	1	Guthrie (1993); Rick et. al. 2009	
Santa Rosa	SRI-1	9390-1980 cal BP	1290-1180; 480-320	9	6	Collins (1991a); Rick et al. 2009	2
	SRI-2	2460-Historic	530-480	>16	9	Collins (1991a & b); Rick et al. 2009	5
	SRI-3	8860-2760	310-0	3	2	Collins (1991a); Rick et al. 2009	2
	SRI-4	7560-1830	660-550	1	1	Collins (1991a); Rick et al. 2009	1
	SRI-25	n/a		2	1	Shelley (2001); Rick et al. 2009	-
	SRI-41	5610-1040	3830-3640	2	1	Collins (1991a); Rick et al. 2009	1
	SRI-168	Late Holocene		2			1
	SRI-347	n/a		1			-
	SRI-365	n/a		n/a	1	Rick et al. 2009	-
	SRI-670	Late Holocene		2			2
	SRI-XX	n/a		n/a	n/a		3
	Upper Tecolote	Terminal Pleistocene	1510-1280	3	1	Collins (1991a); Shelley 2001; Rick et al. 2009	1

Santa Cruz	SCRI-1	2670-Historic		2			2
	SCRI-122	Late Holocene		2	2	Collins (1991a); Rick et al. 2009	-
	SCRI-131	Late Holocene		2	2	Collins (1991a); Rick et al. 2009	-
	SCRI-147	Late Holocene		>18	5	Collins (1991a); Rick et al. 2009	-
	SCRI-206	n/a		1	1	Collins (1991a); Rick et al. 2009	-
	SCRI-236 (SCRI-86)	5320-500		7	6	Collins (1991a); Rick et al. 2009	-
	SCRI-240	5570-320		5	n/a	Noah (2005); Rick et al. 2009	-
	SCRI-257	Late Holocene		4			4
	SCRI-306	760-270		n/a	n/a	Arnold (1987); Rick et al. 2009	-
	SCRI-328/330	910-Historic		9	n/a	Noah (2005); Rick et al. 2009	-
	SCRI-333 (SCRI-3)	6280-1090	6180-5950; 2750-2510	45	13	Collins (1991a); Rick et al. 2009	2
	SCRI-474 (SCRI-100)	Late Holocene		>46	11	Collins (1991a); Rick et al. 2009	-
	SCRI-496	Late Holocene		4			2
Anacapa	ANI-2	3250-2710	3210-3010	1		Reeder and Rick 2009; Jew et al. 2015	1
San Nicolas	SNI-7	n/a		n/a	20	Collins (1991a & b); Rick et al. 2009	13
	SNI-11	7160-330	5070-4790	>5	2	Collins (1991a); Rick et al. 2009	-
	SNI-16	Late Holocene	1870-1730	n/a	n/a		3
	SNI-25	740-Historic	530-490; 500-320	n/a	10	Rick et al. 2009	9
	SNI-51	2870-1720		2	1	Collins (1991a); Rick et al. 2009	-
	SNI-102	2870-2440		n/a	n/a	Martz (2005); Rick et al. 2009	-
	SNI-119	n/a		4	1	Collins (1991a); Rick	-

						et al. 2009	
	SNI-160	1810-800		n/a	n/a	Martz (2005); Rick et al. 2009	-
	SNI-161	5450-4710		1	1	Vellanoweth (1998); Rick et al. 2009	-
San Clemente	SCLI-43	12,540-510	2200-2300; 1810-1610	>28	4		1
	SCLI-48	n/a		1	1	Collins (1991a); Rick et al. 2009	-
	SCLI-1215	5440-310		>2	2	Collins (1991a); Rick et al. 2009	-
	SCLI-1531	n/a	530-490	3			1
	SCLI-1524	2360-Historic	540-500; 430-150: 300-0	8		Collins (1991a); Rick et al. 2009	3
Santa Catalina	SCAI-17	5990-4270; 1520-470	5460-5310	3	2	Collins (1991a); Rick et al. 2009	1
	SCAI-26	720-Historic		22		Porcasi 2012	-
	SCAI-32	Late Holocene		51		Porcasi 2014	-
	SCAI-137	Historic		3	1	Collins (1991a); Rick et al. 2009	-
						Total	***64***

Island Fox $\delta^{13}C$ and $\delta^{15}N$ Values

We examined the possibility of human provisioning in fox populations by comparing island fox, dog, and human isotope values (Figure 4.3). While archaeological human data are not available on San Miguel, Anacapa, and Catalina, human diet varies considerably (-19.9 to -8.7 for $\delta^{13}C$, 4.4 to 23.0 for $\delta^{15}N$), especially on the mainland where terrestrial resources likely make up a larger component of the diet. On the islands, isotopic signatures confirm that ancient peoples consumed a large amount of marine resources supplemented by plant resources like corms (see Gill 2014). Ancient dogs from San Clemente, San Nicolas and Santa Rosa cluster closely with humans while island fox

signatures are more distinct. Most island foxes differ from human dietary estimates although there is variation between islands and time points (Figure 4.3 and 4.4). Island foxes on San Nicolas demonstrate the most variation in diet and evidence of provisioning (Figure 4.5). Several individuals on San Nicolas, Santa Rosa and San Clemente foxes show similar values as humans (Figure 4.3). Juvenile fox burials from San Clemente also exhibit a weaning signature (Figure 4.2).

Stable isotope patterns in foxes differ significantly between islands ($\delta^{13}C$ F= 9.052, P<0.001 and $\delta^{15}N$ F=24.35, P< 0.001) and time period on Santa Cruz ($\delta^{13}C$ F= 6.846, P<0.01 and $\delta^{15}N$ F=4.059, P< 0.05) and San Nicolas ($\delta^{13}C$ F= 12.87 P<0.001 and $\delta^{15}N$ F=26.32, P< 0.001) and just in $\delta^{13}C$ on Santa Catalina ($\delta^{13}C$ F= 5.561, P<0.05), San Clemente ($\delta^{13}C$ F= 7.119, P<0.01), and San Miguel ($\delta^{13}C$ F= 4.563, P<0.01). On the northern islands, small differences in trophic level can be detected on San Miguel where late and middle Holocene foxes are enriched in nitrogen (Figure 4.4). On Santa Cruz and Santa Rosa, there is little difference between time periods though Santa Rosa shows more variability in the 1800s. The southern islands show a dramatically different pattern. On San Clemente, archaeological, historic and recent foxes are eating much higher amounts of nitrogen than the northern islands. Late Holocene samples in particular document a unique signature with a $\delta^{13}C$ mean of -19.0 ‰ and $\delta^{15}C$ mean of 14.9 ‰ (Appendix B, Table S2). Late Holocene foxes on San Nicolas are enriched in ^{13}C relative (mean $\delta^{13}C$ = -15.8) to late Holocene San Clemente foxes but exhibit similar patterns in nitrogen (mean $\delta^{15}C$=14.9). Santa Catalina foxes show a slight increase in carbon between the 1800s and 1900s and are very similar to Santa Cruz in trophic level. The best evidence for a

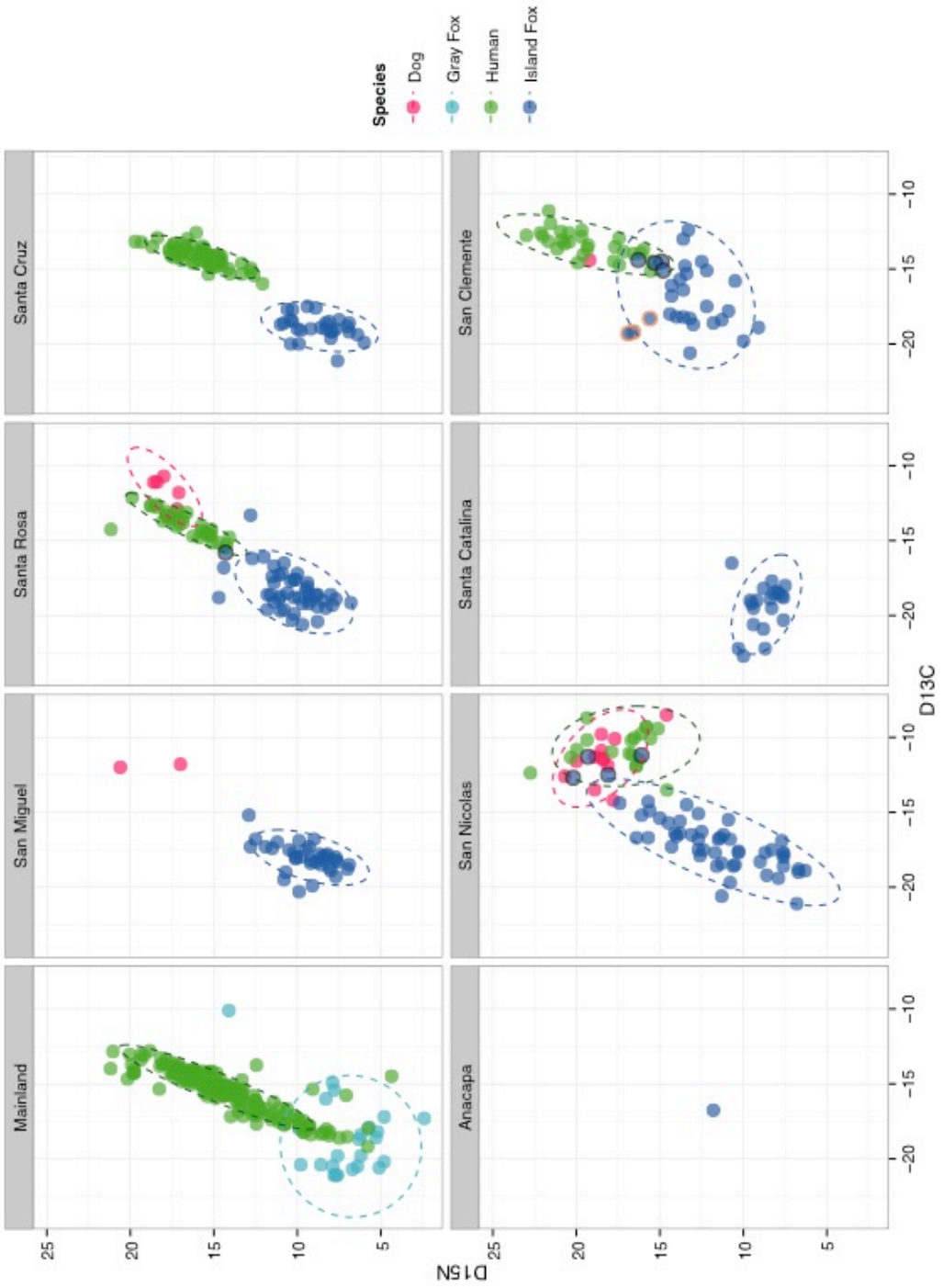


Figure 4.3 Stable Isotope Plot of Archaeological Humans, Archaeological, Historic and Modern Island foxes and Modern gray foxes. For each species, 95% confidence intervals are shown and island foxes within the 95 % human confidence interval are outlined in black and juveniles with weaning signatures are outlined in orange.

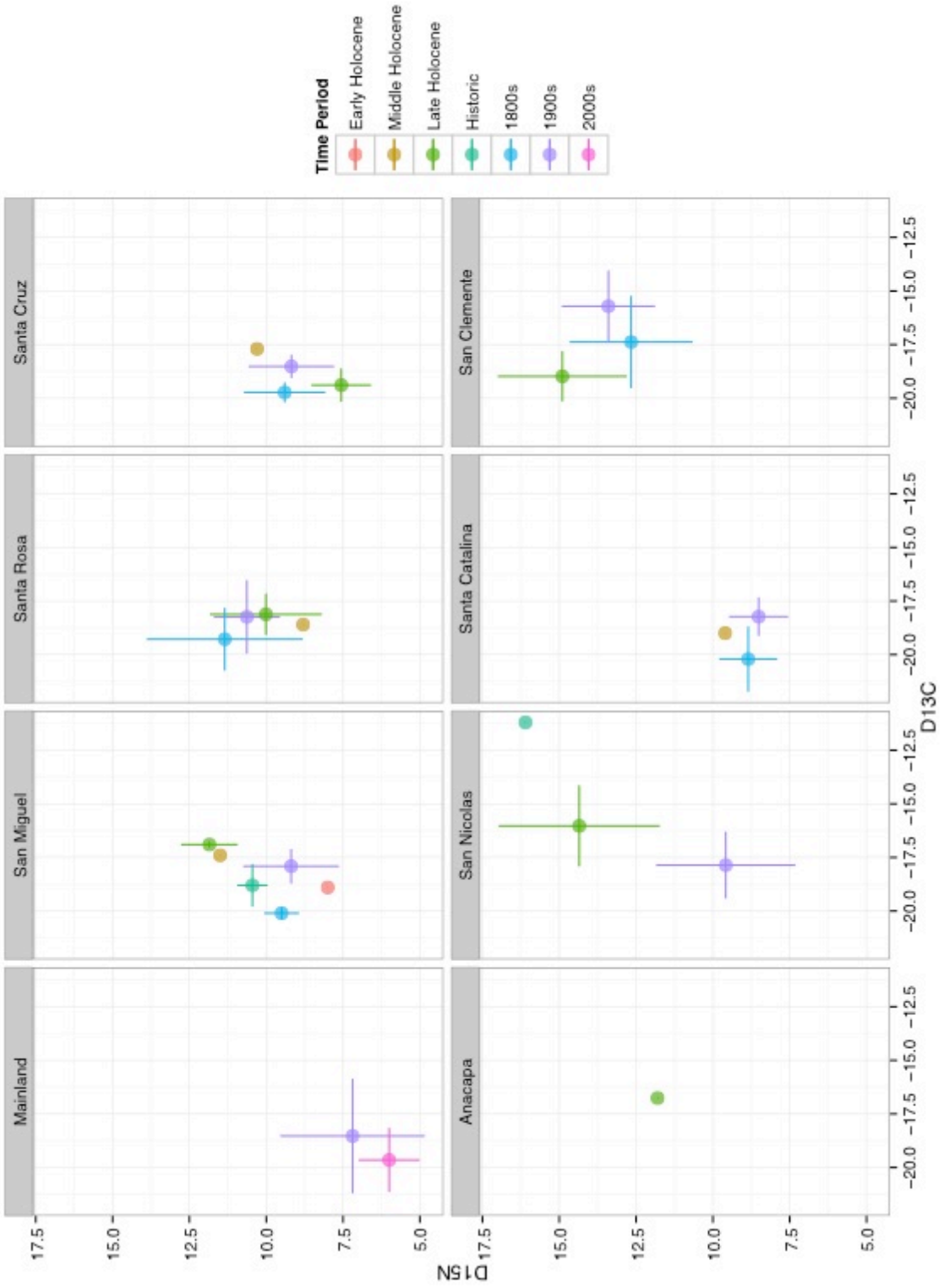


Figure 4.4 Stable isotope plot of island and gray fox mean carbon and nitrogen by time period.

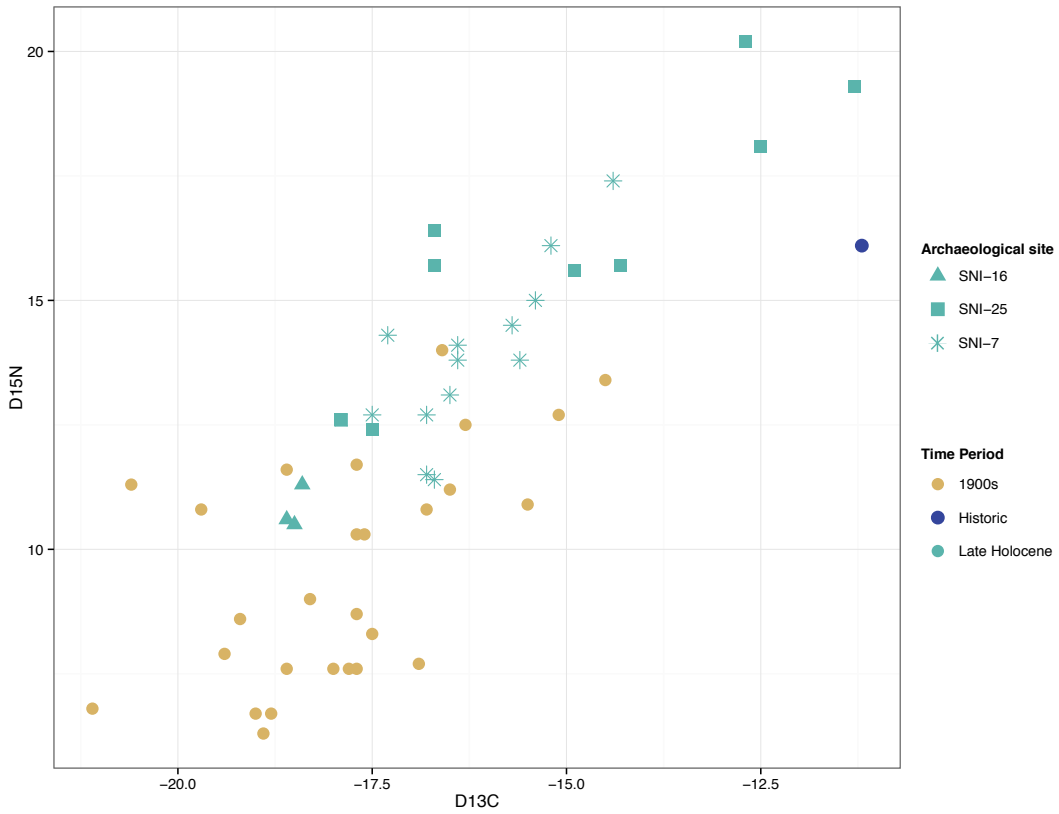


Figure 4.5 Human Provisioning on San Nicolas. Island foxes on San Nicolas show evidence of provisioning in the late Holocene.

temporal change in diet comes from San Nicolas where late Holocene foxes are eating at a significantly higher trophic level than in the 1900s (Figure 4.4 and 4.5).

Discussion

Island Fox Chronology

We identified and dated all potentially early island fox remains and none are older than 7310 cal BP, which supports the pattern found by Rick et al. (2009) that directly dated a smaller number of ancient island foxes. While it is likely that we have not dated the first fox on the Channel Islands, our data support an arrival during the end of the early Holocene. Extensive survey, excavation, and analysis of the late Pleistocene and early

Holocene archaeological contexts of the northern Channel Islands (Erlandson et al. 2011; Rick et al. 2013) as well as paleontological fossil localities have yielded no other evidence of foxes. Rick et al. (2009) noted that many of the Channel Islands fossil localities were thought to be ancient bald eagle nests that likely would have contained fox remains if present. Especially since island fox remains are occasionally found in modern bald eagle nests today (Newsome et al. In Press). The oldest date of ~7300 years also fits well with genetic estimates of island and gray fox divergence. Analysis of mitochondrial genomes calibrated with a slightly younger date (7160-6910 cal BP), suggested that island foxes diverged from their mainland progenitor ~9200-7100 cal BP. This is well after humans first arrived on the Channel Islands (~13,000 cal BP), but it is still unclear exactly how (natural dispersal and/or human-assisted) foxes first arrived on the islands.

Our oldest island fox remains come from San Miguel Island (Figure 4.2A) and support the arrival of foxes to the northern islands and subsequent introduction to the southern islands. Two dates from San Miguel (7310-7170 and 7160-6910 cal BP) predate any dates from the southern islands by approximately 2000-1500 years. Foxes may have dispersed naturally to the northern islands during the human era, or been introduced by Native Americans. Depending on when foxes arrived on the northern islands, sea level could have impacted their dispersal between islands. The northern islands coalesced into a super-island, Santarosae (see Figure 4.1), that began to separate into the modern configuration around 11,000 cal BP and was completely separated by 9000 cal BP (Reeder-Myers et al. 2015). The early fox AMS dates put the arrival of foxes well after the islands separated, but genetic estimates of divergence between island and mainland populations are just before or just after the islands broke in separate masses. If foxes

arrived after the islands separated, than the most parsimonious explanation for their distribution is a translocation by ancient peoples between the northern islands.

The first evidence of foxes on the southern islands comes from Santa Catalina and San Nicolas and dates to 5460-5310 and 5070-4790 cal BP, respectively. Genetic estimates suggest that southern island lineages diverged from northern lineages shortly after foxes arrived on the islands (Hofman et al. 2015). As rafting to three additional southern islands that are further from the mainland than their northern counterparts is unlikely, genetics and AMS dates suggest that ancient peoples quickly moved foxes to the southern islands following their initial arrival.

While investigating the contexts of all recorded island fox material, we documented considerable variation between previously reported site chronologies and AMS dates on island fox bones recovered from the site. For example, 15 AMS dates from SRI-3 suggest a trans-Holocene occupation from 8860-2760 cal BP, but the island fox remains from the site were directly dated to ~300 years ago. A similar pattern of deviation between known site chronologies and direct island fox dates was also identified at SRI-1 and SRI-4 (Table 4.1). Previous analysis of island foxes from subfossil localities reported to be 40,000 and 16,000 years old documented the same problem as all fox remains from these subfossil localities were dated to the Holocene and even historic times (Rick et al. 2009b). Much of the problem stems from the fact that these subfossil and the archaeological specimens noted above were obtained from the surface of a site or from an unknown locality rather than in good stratigraphic context. In one case, fox remains recovered by Orr (1968) at a subfossil locality on Santa Rosa Island were argued to be at least 16,000 years old. These data were used to support a pre-human colonization

of the northern Channel Islands by foxes (Collins 1991a; Orr 1968) and were used to calibrate many of the initial genetic studies of foxes (Aguilar et al. 2004; Gilbert et al. 1990; Wayne et al. 1991). Direct AMS dating of this bone indicated that it was only 1200 years old and likely from a fox that had intruded into Pleistocene deposits (Rick et al. 2009b; Shelley 2001). Consequently, we advocate for direct AMS dating of island foxes and other animal bone samples, especially when making interpretations about species chronology or dispersal patterns.

Ancient Island Fox Diets

Early and Middle Holocene

We explored changes in island fox diet spanning 7300 years and seven islands, including Anacapa where foxes had not been previously reported. We hypothesized that if humans introduced foxes to the northern islands, early fox remains from the northern islands might show signatures of human provisioning. The earliest fox from San Miguel does not have a provisioning signature, but rather appears to have a strict terrestrial diet, much more so than foxes in later periods of time (Figure 4.2). On Santa Cruz, a middle Holocene (6180-5950 cal BP) fox has higher $\delta^{13}C$ and $\delta^{15}N$ values relative to younger foxes, but there is no definitive evidence of provisioning on Santa Cruz. On the southern islands, the earliest fox on Catalina may be slightly enriched relative to later periods but human data are not available from Catalina so it is difficult to make an assessment of provisioning. The earliest foxes from San Nicolas were not sampled for isotopic analysis so it is unknown what the earliest fox recorded on San Nicolas might have been eating. Together these few data points suggest that ancient peoples were not provisioning early and middle Holocene island foxes. Although we do not detect human provisioning as

evidence for an ancient human introduction in these samples, we caution that the data do not preclude a human introduction.

One explanation for why humans would translocate foxes to the Channel Islands was for pest management, or to help keep deer mouse populations in check on an island with few natural predators (Collins 1991a; Rick et al. 2009b; Vellanoweth 1998). If this was a factor in translocation then we would expect fox diets to not indicate provisioning. Competition with dogs may have also forced many foxes to focus on deer mice and other wild foods. Even if ancient peoples were not provisioning foxes directly, midden refuse could have attracted mice, a fox dietary staple (Cypher et al. 2014).

Late Holocene

In the late Holocene (3500-200 cal BP), we detect human provisioning of island foxes on Santa Rosa and San Nicolas. On Santa Rosa, the provisioned fox comes from the Upper Tecolote member and dates to 1510-1280 cal BP (Figure 4.3). Human population sizes on the islands increased during the late Holocene as people settled in sedentary villages with as many as 1000 people (Kennett 2005). Higher population densities producing more refuse could provide a valuable resource for island foxes living in close proximity to a village. It is difficult to distinguish between scavenging from human refuse and intentional human provisioning but either way, humans may have been influencing fox diet.

San Nicolas has considerable variation in trophic level in the late Holocene with $\delta^{15}N$ and $\delta^{13}C$ values differing between by 9.7‰ and 7.3‰ respectively. We detected four foxes with human provisioning signatures, all of which come from the Tule Creek Village site (SNI-25). The east locus of SNI-25 has a number of features associated with

ceremonial events including shell effigies, feasting pits, and animal burials (Smith 2013). Three disarticulated foxes from the east locus have higher $\delta^{15}N$ (mean 19.2 ‰) and carbon (mean -12.2 ‰) when compared to three foxes from the south locus (mean $\delta^{15}N$ 14.57‰; $\delta^{13}C$ = -15.59‰) (Smith 2013). While not within the 95% human/dog confidence intervals, additional late Holocene foxes from SNI-7 also have higher $\delta^{13}C$ and $\delta^{15}N$ values (Figure 4.5). Nearly 20 island fox skulls were excavated at SNI-7, perhaps for production of a fox cape or blanket (Collins 1991b), but little is known about their context. On the southern islands, the *Chingichngish* religion may have played a significant role in these island fox dietary patterns. Described as a crisis religion in potential response to the introduction of European disease and Christian deserters (Jackson and Castillo 1996; Raab and Cassidy 2009), practices included the use of *tolache* (jimsonweed) during an initiation ceremony for young men, formal ritualized ceremonies, and animal sacrifice (Jackson and Castillo 1996; Raab and Cassidy 2009).

On San Clemente, island foxes were recovered from a ceremonial site possibly associated with the *Chingichngish* religion (SCLI-1524). Excavations within the interior of a circular midden berm surrounding a potential *wamkish,* or an open area ceremonial site, yielded 11 canid burials (five dogs and six fox burials) (Hale and Salls 2000). Of the six fox burials, all but one were juveniles and one burial (Feature 6) contained two juvenile foxes. We dated three juvenile foxes and one juvenile dog from these burials and the dates span three non-overlapping time periods (730-670 cal BP (dog), 540-500 cal BP (fox), and 430-0 cal BP (double fox burial). These data suggest that people were likely returning to this site and burying juvenile canids for ~370-580 years. While the youngest fox burial might be associated with the *Chingichngish* religion that developed after

European contact, the site was used well before European contact for ritual animal sacrifices. Hale and Salls (2000) suggest that this site might be part of a long forgotten canine ritual that is not described in the ethnographic record (Hale and Salls 2000).

We detected a weaning signature (Figure 4.2) in the three juvenile fox burials from SCLI-1524. Juveniles typically have higher $\delta^{15}N$ values than adult females (mothers) (Fuller et al. 2006) and the effects of nursing on $\delta^{13}C$ values is unknown in foxes. The young age of these individuals does not allow us to explore human provisioning, but suggests that ancient people either had just taken these juveniles from their mothers or had the mother on hand to feed her offspring. We can also potentially use these data to identify the seasonality of this ritual. Fox pups are born in litters of one to five pups in late April and early May. Fox mothers lactate for 7-9 weeks and pups emerge from the den in the early summer (Moore and Collins 1995). The juvenile foxes from SCLI-1524 are less than two months of age based on dental eruption (Hale and Salls 2000). Therefore this ritual potentially can be dated to June or July, or just as fox pups are emerging from their dens and learning to forage with their parents. These ritual activities on San Clemente and evidence of provisioning on San Nicolas indicate that late Holocene people had considerable interaction with island fox populations.

Historic and Recent Times

Archaeological and late Holocene fox diet differs considerably from 19th and 20th century populations on several of the islands (Figure 4.4). Historic ranching dramatically transformed island landscapes in the 19th century. On San Nicolas, ranching followed by the introduction of non-native grasses to mitigate the resulting erosion, affected island fox diet. With limited native resources, foxes today rely mostly on non-native resources

(Cypher et al. 2014) and their diets differ considerably from late Holocene foxes. On San Clemente, we also identified four foxes with evidence of provisioning all of which date to the late 19th and 20th century (1897; 1977; 1982; 1982). San Clemente has been owned and managed by the Navy since 1934 and it is feasible that foxes may have been provisioned by sailors stationed on the island. There are also anecdotal accounts that historic ranchers kept island foxes as pets and moved foxes from Santa Catalina to San Clemente (Collins 1991a; Johnson 1975). During the course of the twentieth century, human land use shifted from ranching to conservation-oriented management likely causing the minor shifts we see in island fox carbon and nitrogen values.

Human Provisioning or Scavenging?

We detected no evidence of potential human resource provisioning of foxes on the Channel Islands except late Holocene San Nicolas and Santa Rosa and historically on San Clemente. Human isotope values on the Channel Islands have mean values of -13.5 ± 1.4 in $\delta^{13}C$ and 16.9 ± 2.2 in $\delta^{15}N$ and enrichment in fox bone collagen to these levels would necessitate the consumption of considerable marine resources. We also included at least 25 archaeological foxes from burials and/or human cemetery associated contexts (Collins 1991b) in this study to compare intentional burial of foxes with midden contexts. The majority of these are from SNI-7 (n=13), where context information is limited, and SCLI-1524 (n=3) where the three samples were juveniles and cannot tell us about human resource provisioning. The SNI-7 foxes show considerable variation in nitrogen (11.4 to 16 ‰) and less in carbon (-17.5 to 15.2 ‰) near human ranges (Figure 4.5), but the potential burials or cemetery associated foxes from SRI-1, SRI-2, SRI-41, SCRI-1, and SCRI-257 do not show the same patterns (Rick et al. 2011a). Foxes from SNI-25 also

have distinct isotope values (Figure 4.5) which may be associated with the late Holocene *Chingichngish* religion.

While these high carbon and nitrogen values in foxes could be a result of intentional or unintentional provisioning, they might also be generated through scavenging of marine mammal carrion. However, we found little evidence of considerable marine input (> 15 $\delta^{15}N$) in bone collagen of recent fox populations from San Miguel and San Nicolas where there are large marine mammal rookeries. More data on the location and home range of each provisioned fox and comparisons between bone collagen of foxes known to scavenge marine carrion would be necessary to eliminate marine mammal scavenging as a cause of the provisioning signature.

Long-Term Trends

With a dataset spanning 7300 years and a number of different human land use practices, from hunter-gatherers to ranching and now conservation-oriented management, we are able to identify some important long-term trends. Island foxes have great dietary breadth and diet varies substantially between islands and in some cases through time. Long-term patterns in stable isotopes are most similar on Santa Catalina and Santa Cruz (Figure 4.4). Interestingly, in a pairwise analysis of modern scat content, Horn's similarity index (0.59) shows that these islands are similar today as well (Cypher et al. 2014). A recent translocation event from Santa Cruz to Santa Catalina was detected by mitogenome network analysis. These patterns could be a result of the introduction of Santa Cruz foxes with prey preferences to Catalina in the recent past or similar environmental conditions on the two islands. More research is needed to evaluate if foxes

with the Santa Cruz mitochondrial haplotype are driving the dietary patterns seen in island fox scat.

Regardless of time period, San Clemente has enriched carbon and nitrogen relative to the other islands (Figure 4.4). Two scenarios explain this pattern: 1) There are environmental differences between San Clemente and the other islands impacting resource availability and prey choice or 2) People have provisioned foxes from the late Holocene through the present. We do not have earlier data points to compare what fox diet might have looked like prior to ~ 2300-2200 cal BP before population increases and the onset of the *Chingichngish* religious practices. San Nicolas shows a clear trend (Figure 4.5) with a decrease in $\delta^{15}N$ and $\delta^{13}C$ values between the late Holocene and the 1900s. This island has the best evidence for potential Native American provisioning of foxes, and also shows that fox diet changed dramatically in the wake of early 19th century removal of Native Americans from the island.

Conclusions

In this study, we describe spatial and temporal variation in how humans interacted with fox populations. Early foxes from the islands do not show a signature of provisioning and we were not able to discern if foxes arrived on the islands by rafting or by human introduction using stable isotopes. However, we were able to identify a number of unique human-fox interactions. Ancient peoples likely ritually sacrificed juvenile foxes on late Holocene San Clemente; on San Nicolas and possibly Santa Rosa, there is evidence of resource provisioning of adult foxes; although, we do not detect significant human-fox interactions using isotopes on other islands, more than 50 intentional fox burials show a ritual interaction between humans and foxes.

Ancient island foxes exhibit substantial dietary variation spanning several trophic levels and have weathered considerable environmental perturbations including dramatic cultural and landscape changes. These data are important for the ongoing conservation and management of the endangered carnivore. While the Channel Islands have limited terrestrial resources, continued management for native plants and wildlife will be important as predicted climate change impacts island biodiversity (Rick et al. 2014). Stable isotopes show that island fox populations are relatively adaptable to a number of environmental conditions and food resources. It remains to be seen whether island fox populations will be able to adapt to future climatic and cultural changes and careful monitoring and management will be required.

Chapter 5: Conclusions and Broader Implications

Future Directions and Outstanding Questions

Human behavior has dramatically altered the planet during the Anthropocene through domestication, overharvest, landscape clearance, translocations, pollution, and extinction. As we work to mitigate anthropogenic changes through conservation and management actions, knowing how environments have changed in the past is important for setting appropriate restoration targets. Interdisciplinary datasets are critical to understanding the long-term trajectories of the world's ecosystems and the archaeological record, or the outcome of human activities, is a valuable resource for understanding human-environment relationships through time and across space (Lyman 2012; Rick and Lockwood 2013; Wolverton and Lyman 2012).

While recent anthropogenic environmental impacts are clear, ancient peoples have also impacted the environment in unexpected ways (Grayson 2001; Hughes 2009; Redman 1999). Ancient peoples significantly impacted species distributions through intentional and unintentional movement of wild and domestic plants and animals around the world (Grayson 2001; Jones et al. 2013; Storey et al. 2013). Translocations by ancient peoples have blurred our understanding of what is natural, native, and endemic. They also complicate management decisions about what an ecosystem or environment should look like following restoration. Using the framework of historical ecology, I investigated the role ancient and modern peoples played in the construction of California Channel Island ecosystems by examining the evolutionary history and long-term foraging ecology of endemic island fox. The goal of this dissertation was to integrate archaeology, stable isotopes, AMS radiocarbon dating, and genomics to explore the impact ancient peoples

have had on biodiversity and help enhance the development of conservation, restoration, and management goals for biodiversity in the face of future uncertainty.

In chapter two, I identified five areas in which archaeogenomic data can address important problems we are facing in the Anthropocene: extinction, range shifts, translocations, and disease. And lastly, I described how reconstructing paleoecosystems is an important component of conservation archaeogenomics as understanding past ecological perturbations and variability will allow us to better plan for the future. This study demonstrated that archaeological materials and scientific methods including AMS dating, stable isotopes, and zooarchaeology, are valuable tools that can be integrated with genetic analysis to examine past and present anthropogenic change in the environment.

In chapters three and four, I presented case studies focusing on how humans, past and present, have influenced the biogeography and evolution of an island endemic mammal, *Urocyon littoralis*. My three objectives were to 1) resolve the evolutionary relationship between island and gray foxes, 2) evaluate the relationships between island populations, and 3) explore human impacts on fox diet through time and across space. I addressed objectives one and two in my third chapter. I sequenced mitochondrial genomes from 185 island and gray foxes and conducted phylogenetic analyses to explore the evolutionary relationship between island and gray foxes. These data suggest that island foxes diverged from mainland gray foxes ~9200-7100 years ago, several thousand years after people first reached the islands (Hofman et al. 2015). While these analyses were not able to demonstrate how (natural, human assisted, or combined) foxes first arrived on the islands, the results do suggest that ancient peoples moved the fox from one island group to the other soon after their arrival. I was able to resolve the relationships

between extant island populations and presented evidence of a recent translocation from Santa Cruz to Santa Catalina islands and the possibility of a bottleneck before 2300 cal BP.

In chapter four I addressed objective three by utilizing the Canine Surrogacy Approach to explore how ancient peoples may have influenced island fox diet over 7300 years. I showed that island foxes may have been provisioned on Santa Rosa and San Nicolas in the late Holocene and historically on San Clemente. I also described several other human-fox interactions including the sacrifice of juvenile foxes on San Clemente. The results of the analysis of stable isotope data demonstrate that foxes have adapted to the islands through considerable environmental and cultural change. Understanding the variability in which fox populations can survive is important as they are conserved and protected for future environmental change and other anthropogenic perturbations. Together chapter three and four try to address how ancient and modern peoples influenced island fox biogeography and suggest that foxes may be in a symbiotic or commensal relationship with humans during parts of their history on the islands.

In this concluding chapter, I describe ongoing research and outstanding questions that I identified during the course of these projects. I have identified seven important questions that need additional investigation: 1) How did foxes arrive on the Channel Islands? 2) Why were they moved between islands? 3) Were island foxes semi-domesticated? 4) Do nuclear genome data align with mitochondrial genomes? 5) Do the climate-induced phylogeographic patterns in California extend to the rest of the gray fox range? 6) How can these genomic resources be applied to population monitoring? 7) How have historic anthropogenic changes influenced island fox biology? My collaborators and

I are exploring these questions with a number of techniques including ancient DNA, whole genome sequencing, trace element analysis, and sequence capture.

Ongoing Projects and Future Research

Archaeogenomics and SNPs

The analysis of AMS radiocarbon dates, stable isotopes, and mitochondrial genomes of island fox populations suggest that foxes arrived on the Channel Islands between 9200 and 7300 years ago (Hofman et al. 2015). While these data help understand when foxes arrived, they do not tell us precisely how foxes arrived on the islands. The fact that foxes arrived to the Channel Islands during the human era, were quickly transported to the other islands, and had close relations with Native Americans all support a human introduction of foxes to the Channel Islands. Ongoing research is using ancient DNA to help further unravel the origins of the island fox and alleviate the confounding effects of recent population crashes leaving as few as 15 individuals on some islands during the 1990s. Recent bottlenecks with fast recoveries are very difficult to detect but ancient samples can improve our ability to identify past demographic events (Mourier et al. 2012). Ongoing research on ancient (n=64) and historic (n=159) island and mainland foxes spanning 7300 years will aid in investigating the population dynamics of foxes during the Holocene. Archaeogenomic research is focused on capturing mitochondrial genomes from bone samples. This research is in the final stages and will be completed in the Summer 2015.

While the results presented in this dissertation focus on mitochondrial DNA data, nuclear loci are important for investigating introgression and species delimitations. Island and gray foxes are currently separate species and there are distinct subspecies on each of

the six Channel Islands with foxes. Introgression between island and mainland localities is possible and nuclear data will allow us to determine the potential for recent and historical migrants. SNP data have been generated from island and gray fox populations from across California using a RAD approach and will be submitted by my collaborator W. Chris Funk (Colorado State University) to *Molecular Ecology.* Additionally, I have designed RNA probes from these markers to design a capture hybridization array to conduct a comparative study between RAD and sequence capture approaches for SNP analyses. These same capture hybridization arrays are also being utilized in the high quality archaeological and historic samples to develop a comparative archaeogenomic dataset.

In chapter three, I concluded that a phylogeographic study across the range of gray foxes is necessary as there are considerable levels of genetic divergence between fox populations on the east and west coasts. Planning for this study is underway and will use the same SNP and mitochondrial markers from our investigation of California foxes so that data are comparable range-wide. A pilot study in the Summer of 2015 will examine potential ascertainment bias in using these SNP markers on eastern gray fox samples and generate preliminary range wide data. Several subspecies of gray foxes in the Midwest have shown declines, with hunting currently allowed in some states. The prairie gray fox subspecies is being considered for listing under the Endangered Species Act and a phylogeographic review will be important in informing conservation practices.

Human Fox Interactions

The archaeological record of the island fox reveals a complex relationship with humans during the course of their history. Island fox remains have been identified in both

intentional burials and in midden and subfossil contexts suggesting varying relationships with humans (Collins 1991b). Intentional burials, with grave goods in some cases (Collins 1991b; Hale and Salls 2000; Rick et al. 2009b), indicate a reverence for the species. Ethnographic data from early expeditions to the islands describe a "Fox dance" in which participants wore several possible headdresses: a tule frame covered in a fox skin or another animal, twined junco wrapped around the head with a long braid down the back made of rags covered in flowers and weighted by a rock or their hair was tied in horns with a animal skin tail (Hudson 1985: 195). Little is known about the dance but it was performed by historic Channel Island peoples (Hudson 1985). In contrast, both dogs and foxes have been found in middens on nearly all of the islands indicating they may not have had the same importance to people. Stable isotope data support a complex relationship with considerable temporal and spatial variation in dietary signatures. While there is some evidence of human provisioning from several islands, for the most part, long-term patterns show that island foxes were primarily eating an omnivorous diet with terrestrial resources.

One of the outstanding questions from this research is whether human selection influenced island fox evolution. The behavioral, morphological, and genetic changes seen in island foxes may be a result of living on islands with few predators for several thousand years or it could be due to human selection or a combination of the two possibilities. While we argue that humans played a role in island fox dispersal and there is some evidence of selection in modern island and mainland fox populations (dn/ds ratios), we cannot conclusively determine that these changes between island and mainland populations are the result of human selection. To investigate the role of human

mediated selection, we are sequencing 45 island and gray fox genomes with 5x coverage and aligning the data to the well-annotated dog genome. The goal of this study is to identify regions of high F^{st} and reduced heterozygosity in 500 kb regions between island and mainland populations as locations of potential selective sweeps. Genomic regions with high Fst may be under selection (human or natural) or could also be a result of a small founding population. To disentangle these scenarios, we will compare gene ontology of genes within these regions to other taxa that have undergone domestication. The same genome analytic methods are being used in populations of rats and mink that have undergone rapid domestication from the same source population and have identified several genomic regions that appear to be consistently under selection during domestication in different species (Alex Cagan- personal communication). We hope to be able to use these known regions as markers to explore the possibility of human selection on the island fox genome and further evaluate the core questions of this dissertation.

While I focus on island fox chronology, origins, and interactions with humans, the reasons why ancient people might have translocated foxes are still unknown and needs further investigation. One potential explanation is that foxes could fill a pest control niche. Modern island fox populations eat a high proportion of deer mice on all islands (Cypher et al. 2014) and ancient peoples may have introduced the fox to reduce mice populations in the middens near their households. Dogs and deer mice (*Peromyscus maniculatus)* also arrive on many of the islands in the middle Holocene. While dogs occasionally do kill rodents, foxes would likely be better pest management tools. Another potential motive for the movement of foxes is ritualistic. Intentional burials by the

Chingichngish relgion on the southern islands indicate that there was a ritual component to the human-fox relationship in the Late Holocene.

Ecotoxicology

Another important consideration for understanding island fox evolution is the role that environmental contaminants could have played in population demography and evolution. Environmental contaminants, especially heavy metals, can decrease fertility, birth rate and increase mutation rates influencing genetic diversity and population demographics (Bickham et al. 2000). Bone tissue acts as an important reserve of essential elements and nutrients for the body, and as a physiological sink for heavy metals such as lead (Pb), mercury (Hg), and cadmium (Cd) (Brodziak-Dopierala et al. 2009). These metals can be absorbed by the body via food, drinking water, and polluted air, and accumulate in bone over long periods of time. Due to the low turnover rate of bone, concentrations of metals in the skeleton can reflect an organism's cumulative lifetime exposure to these elements (Honda et al. 1986a,b). Furthermore, because they are often well-preserved long after death, human and animal bones can provide a record of environmental metalloid pollution in the past and present (Degryse et al. 2004; Ericson et al. 1979, 1991; Kuo et al. 2000; Martiniaková et al. 2011, 2012; Vuorinen et al. 1990).

Following previous studies that have used fox (*Vulpes*) bones as indicators of metal contamination in the environment (Budis et al. 2013; Lanocha et al. 2012, 2013; Naccari et al. 2013), we are focusing on island foxes as they are one of the only terrestrial predators on the Channel Islands. We are planning to use the same island fox bone samples from chapter four of this dissertation for this study of environmental contamination. This is an unprecedented dataset for interdisciplinary analysis with bones

from 64 archaeological individuals, nearly 40 19th century and more than 150 20th century samples. Using these samples, we can quantify pre-industrial metal concentrations at many time points across the Holocene and correlate it with genetic data to investigate the effects of heavy metal contamination on island fox genetic diversity and demography. As we move forward with this project, we will be able to develop a long-term pollution history of southern California and integrate these interdisciplinary datasets to explore the relationships between contaminant exposure, diet, and genetic structure in animal populations of the Channel Islands during and outside of the Anthropocene. Ultimately, this will complement genetics and stable isotopes research and provide long-term information on the effects of environmental contaminants on fox evolution, ecology, and conservation.

Broader Impacts

The genomic markers developed during this project are important for continued monitoring of island fox. Considerable effort is invested to monitor island fox health and population sizes through annual trapping of transects on each island (Coonan 2012, 2013; Coonan et al. 2010). While some islands like Catalina will have to continue monitoring by trapping due to unique threats including disease transfer from resident pets, other islands may be able to switch to a less invasive monitoring strategy that uses PCR amplified microsatellite loci for individual identification from scat have not been successful due to the limitations associated with the small numbers of loci developed for Island foxes and the low levels of genetic diversity within islands. However, capturing a large panel of genome-wide SNPs in conjunction with disease diagnostic targets, could be a viable way to estimate population size and detect disease threats. A subset of the

genomic markers used in this and ongoing studies should be tested for individual identification and could be validated in the field for high throughput processing of scats for monitoring purposes. Additional capture probes could be designed for diagnosing diseases that fox are susceptible to and that could be detected in scat. This approach would minimize fieldwork and animal handling time as island fox populations recover following the captive breeding program. Occasional trapping would still be necessary for vaccination and radio-collaring sentinel animals, but the extensive trapping could be eliminated with a scat-capture approach. This would be a new approach to monitoring and could greatly reduce the expense of monitoring programs.

The application of genomic research to conservation of an endangered carnivore is an important component of this project. In working closely with managers, I have been able to identify knowledge gaps that managers are interested in addressing. In addition to the origins of the island fox, together we are exploring the genomic underpinnings of two different morphotypes found on Santa Catalina. These morphotypes may be the result of a recent introduction from Santa Catalina to San Nicolas Island. To test this, mitochondrial genomes and a panel of SNPs are being captured from known individuals from each morphotype. Additional collaborative studies with the Nature Conservancy focus on reconstructing paleo-ecosystems through eDNA analysis of stratified soil samples. By reconstructing ancient Channel Island environments we can better understand how ecosystems variability impacted endemics plants and animals, like the island fox. These projects are important because they address needs of the managers and can help managers make decisions to restore and protect this unique archipelago. Together these projects highlight the importance of conservation archaeogenomics and a

transdisciplinary approach for answering complex questions about anthropogenic impacts on biodiversity. Only in tackling the origins of the island fox from many different directions can we address how ancient and modern people have impacted fox biology.

Archaeology's interdisciplinary approach provides a time depth that has become increasingly important for understanding contemporary environmental problems (Lyman 2006, 2011; Wolverton et al. 2011; Wolverton and Lyman 2012). Many landscapes and seascapes face impending sea level rise, overexploitation of resources, pollution, global warming, and the spread of invasive species. In order to predict how they will respond to future changes, we need to reconstruct the structure and function of their ecosystems in the past. Archaeological data is well situated to fill in the gaps in knowledge of the historical and prehistoric environment (Lyman 2011; Rick and Lockwood 2013). Understanding how animal species and humans adapted to and influenced changing environments in the past will inform decisions about protecting, preserving, and restoring biodiversity, and help untangle issues about the inter-relationships between human cultural practices and the natural world.

Appendices

Appendix A

Radiocarbon dating

To help contextualize our genetic data, we obtained radiocarbon dates on three island fox bones (identified through comparative zooarchaeological analysis) from Santa Cruz and Santa Catalina islands (Table S3). Previous ^{14}C analyses of six fox bones from San Miguel, Santa Rosa, San Nicolas, and San Clemente islands have demonstrated that the oldest island fox bones from the Channel Islands come from subfossil and archaeological deposits dated to 7160 cal BP or younger (Rick et al. 2009b; Shelley 2001). The three new ^{14}C dates we report help expand the geographic coverage of island fox ^{14}C ages.

For the three new ^{14}C dates reported here, we removed a small (ca. 1000 mg) fragment of island fox bone using a clean blade on a Dremel tool. These bone fragments, were then sent to the Oxford Radiocarbon Accelerator Unit at the University of Oxford. The bones were pretreated using ultrafiltration techniques and collagen was extracted and analyzed for the ^{14}C date. For additional details see: http://c14.arch.ox.ac.uk/embed.php?File=index.html.

All dates were calibrated using OxCal v. 4.2 (Ramsey 2009, 2013). Because some foxes may have been consuming high amounts of marine resources, which would require a reservoir correction, the ORAU obtained the ^{13}C values for each specimen independently from the radiocarbon analysis. $\delta^{13}C$ values above –11 were given a marine correction(Rick et al. 2009b). One specimen required a **Δ**R correction (261 ±21;(Jazwa et

al. 2012)) and all dates were calibrated using the Intcal13 or Marine13 calibration datasets (Reimer 2013).

Table S3: AMS Radiocarbon dates of island foxes

Locality		Collection	AMS Lab Number	Material Dated	δ13C ‰ VPDB	Conventional radiocarbon age, 14C yr BP ± 1 SD	cal yr BP age range (2 sigma)	Source
San Miguel Island	Locality V-7c	SBMNH	UCIAMS-40173	Bone Collagen	−17.0	6120 ± 25	7160-6910	Rick et al 2009
	Locality V-10c	SBMNH	UCIAMS-38253	Bone Collagen	−18.4	990 ± 15	950–800	Rick et al 2009
	Locality V-11	SBMNH	UCIAMS-38252	Bone Collagen	−19.5	220 ± 15	300–0	Rick et al 2009
Santa Rosa Island	Upper Tecolote Member	SBMNH	UCR-3563	Bone Collagen	n/a	1440 ± 50	1510–1280	Shelley 2001
Santa Cruz Island	SCRI-333	UCSB-Repository	OxA-29196	Bone Collagen	-17.38	5290 ± 30	6180-5955	This Paper
Catalina Island	SCAI-17 Pit7	Catalina Island Museum	OxA-27377	Bone Collagen	-17.64	4636 ±28	5460-5310	This Paper
	SCAI-17 Pit 11	Catalina Island Museum	OxA-27378	Bone Collagen	-10.89	5463 ±30	5470-5640*	This Paper
San Nicolas Island	SNI-11	SBMNH	Beta 106185	Bone Collagen	n/a	4940 ± 50	5070-4790*[†]	Shelley 2001
San Clemente Island	SCLI-43C	CalState-Northridge	Beta 106185	Bone Collagen	n/a	2110 ±50	2300-1950	Shelley 2001

* Indicates marine calibration using the Marine13 calibration curve and a local marine correction (delta-R) of 261± 21. [†]This sample may be older without a marine correction.

Collectively, these data support previous studies, which demonstrated that all known island fox bones post-date human colonization of the Channel Islands (~13,000 cal BP) by a few millennia (Rick et al. 2009b). The oldest date is from San Miguel at ca. 7160 cal BP, with new dates from Santa Cruz at ~6000 cal BP and Catalina at ~5600 cal BP. Whiles these bones are likely not the oldest island foxes, they support a fox arrival after human colonization and provide an independent means to evaluate our genetic estimates of colonization and divergence.

Mitochondrial genomes

185 complete mitochondrial genomes were sequenced from 201 blood and tissue samples (Table S1) extracted using the DNEasy Blood and Tissue DNA kits (Qiagen). Sequencing libraries were prepared with three different protocols on two platforms and identical haplotypes were recovered between platforms indicating minimal bias. The only discrepancy between the three library prep methods was primer bias in samples that were amplified using long-range PCR. These conserved sites were corrected for downstream analysis.

454 Sequencing

Using two sets of primers developed by Sasaki et al. (2005), for 16 samples, long-range PCR products of 7-9 kb were amplified in 25 ul reactions containing 1X LA PCR Buffer (TaKaRa), 0.5 mM $MgCl_2$, 0.4 mM dNTPs, 0.4 mM of each primer, 1.25 U of TaKaRa LA Hot Start Taq (TaKaRa) (Sasaki et al. 2005). Long-range PCR products for each sample were quantified by spectrophotometry (NanoDrop v 2.0) and pooled in equimolar ratios to 500-1500 ng and were sheared on the QSonica Q800R sonicator for

one minute (15 seconds on and 15 seconds off, 25% amplitude) to roughly 400 bp. The pooled sheared sample was prepared for 454 sequencing following magnetic bead purification with an AMPure substitute (2x) (subsequently called SpeedBeads) and eluted in 15ul of ddH20 (Rohland and Reich 2012). Beads were left in the reaction and PEG solution was subsequently used to purify the libraries. Libraries were prepared with a 25 ul blunt end repair reaction of 1X Quick Blunting Buffer (New England Biolabs), 0.1 mM dNTPs, 1ul Quick Blunting Enzyme mix (New England Biolabs). Reactions were incubated at room temperature for 30 minutes and heat inactivated at 70 for 10 minutes. Adapters with individual barcodes were ligated in 54.5 ul reactions of 1x Quick Ligation Buffer (New England Biolabs), 7.4 uM of Adapter A and Adapter B, and 2.5 ul of Quick Ligase enzyme mix (New England Biolabs) (Meyer et al. 2008). Reactions were incubated at room temperature for 20 minutes, cleaned with 2x PEG solution and eluted in 15ul of ddH20. Adapter fill-in was completed in 30 ul reactions with 1X ThermoPol Buffer, 0.25mM dNTPs and 8 U Bst Polymerase and heated to 37 C for 20 minutes and 70 C for 10 minutes. Reactions were cleaned with 2x PEG solution, eluted in 15 ul of ddH20 and amplified with emulsion PCR primers. Libraries were amplified in 50 ul reactions with 1X Phusion High Fidelity PCR Master Mix with HF buffer (New England Biolabs) and 0.6 mM of each forward and reverse primer. Cycling conditions were as follows 98.0°C for 30 seconds, 15 cycles of 98.0°C for 10 seconds, 60.0°C for 20 seconds, 72.0°C for 50 seconds and a final extension of 72.0°C for 4 min. Libraries were cleaned 2x PEG solution and gel extracted in 1.5% agarose gel and MiniElute Gel Extraction Kit (Qiagen). Libraries were quantified using 10 ul reactions of 454 Library Quantification kits (Kapa) and were sequenced on one run of the 454 Jr. (Roche). The

data was demultiplexed using 454 software and quality filtered using PrinSeq-lite v0.20.3 (Schmieder and Edwards 2011). Reads were trimmed and filtered until the mean read quality score was above 20. Three 454 libraries were combined and assembled *de novo* using Mira v3.4.0 to generate a reference of 16,718 bp(Chevreux et al. 1999). The contigs were aligned with MAFFT v7.017 to the red fox and dog genome to generate a complete gray fox mitogenome reference in Geneious v.5.6.4 (Anon forthcoming; Katoh et al. 2002; Katoh and Standley 2013).

Long-Range PCR and Illumina sequencing

An additional 55 samples were prepared for Illumina sequencing following long-range PCR as described above. Long-range PCR products were pooled to 500ng in equimolar rations and sheared using QSonica Q800R sonicator for two minutes (15 seconds on and 15 seconds off, 25% amplitude) to roughly 600 bp and libraries were prepared with iNext dual indexed adapters (Glenn et al. forthcoming) by cleaning with 2.5X SpeedBeads. The ends of sheared pooled samples were repaired in 48 ul reactions with 1X NEB Buffer 2, 0.03 mM dNTPs, and 1.8 U DNA Polymerase I, Large (Klenow) Fragment (New England Biolabs) and incubated for 15 minutes at 25.0°C and 20 minutes at 75.0°C. Samples were cleaned with 2.5X PEG solution and eluted in 25 ul of ddH20. Instead of d-A tailing, we made dC buffer by adding dCTP (Fermentas) to 10x NEB Buffer for a final dCTP concentration of 2mM. d-C tailing 50 ul reaction consisted of 1x NEB Buffer 2 + dCTP, 15 U Klenow Fragment (3'-5' exo) (New England Biolabs) and were incubated at 37.0°C for 30 minutes. Following dC-tailing, libraries were cleaned with 2X PEG solution, eluted in 25 ul of ddH20. A stubby adapter was ligated in 50 ul reactions with the NEBNext Quick Ligation kit following the manufacturers instructions

with 0.1 uM of stubby adapter and incubated for 15 min at 20.0°C and 10 minutes at 65.0°C. The reactions were cleaned with 2x PEG solution and suspended in 25 ul ddH20. Each sample was amplified in 50 ul reactions of 1x Kapa HiFI Hot Start ReadyMix, 0.5 uM of each i5 and i7 indexing primer and 10 ul of ligated sample. Cycling conditions were 45 seconds at 98.0°C, 15 cycles of 15 seconds at 98.0°C, 30 seconds at 60.0°C and 30 seconds at 72.0°C, followed by 3 minutes at 72. Libraries were cleaned with 2X PEG solution, eluted in 25 ul of ddH20 and quantified using 10 ul reactions of the Illumina Library Quantification kit (Kapa). Libraries were pooled in equimolar ratios for sequencing in one 100 BP paired-end Illumina HiSeq lane. Reads were demultiplexed allowing for one mismatch using CASAVA v1.8.0.

Capture and Illumina sequencing

Based on the 454 dataset, 658 80bp probes with 2x tiling were designed to capture the variation in nine island and mainland mitogenomes generated from 454 data. The RNA probes were synthesized in the MyBaits-1 kit (Mycroarray) for in-solution capture (MitogenomeProbes.fa). Genomic DNA was sheared using QSonica Q800R sonicator for 2 minutes 15 seconds (15 seconds on and 15 seconds off, 25% amplitude) to roughly 600 bp and 130 libraries were prepared with Nextera-style dual indexed adapters as described above. Libraries were pooled in groups of 6-8 individuals and captured for 24 hours following the manufacturer's protocol and were eluted in 30 ul of ddH20. Post-capture the libraries were amplified in 50 ul reactions with 1x Kapa HiFI Hot Start ReadyMix, 0.5 uM of each Illumina primer and 10 ul of captured sample. Cycling conditions were 45 seconds at 98.0°C, 10-16 cycles of 15 seconds at 98.0°C, 30 seconds at 60.0°C and 30 seconds at 72.0°C, followed by 3 minutes at 72. Libraries were

quantified using 10 ul reactions of the Illumina Library Quantification kit (Kapa) and pooled in equimolar ratios for sequencing in one 100 BP paired-end Illumina HiSeq lane. Reads were demultiplexed allowing for one mismatch using CASAVA v1.8.0.

Data filtering and assembly

All 454 and Illumina data were trimmed and quality filtered using the PrinSeq-lite v0.20.3 so that the mean read quality was above 20 on the phred scale. Filtered data was mapped with BWA v.0.7.4 to the gray fox reference and a consensus sequence and coverage information were generated using SamTools v0.1.19 (Li et al. 2009; Li and Durbin 2010). Alignments with ambiguous bases were visually examined and all samples with missing data (n= 14) were removed. An additional two samples were removed following Sanger sequencing.

Consensus sequences for each individual were aligned with Mafft v7.017 as implemented in Geneious 7.06 (Anon forthcoming; Katoh et al. 2002). A highly repetitive region in the control region was deleted in all samples due to mapping and assembly problems with repetitive runs. The resulting alignment of 185 fox mitogenomes of 16,470 bp each totals over 3 million basepairs.

Sanger sequencing verification

For ambiguous sites and haplotypes represented by a single individual, 8 pairs of primers (Table S4) were designed in Primer3 to confirm the base call (Rozen and Skaletsky 1998).

Table S4. Primer sequences

Primer	Sequence
30240A_L	CATACCCCGAAAATGTTGGT
30240A_R	GGCGATGGAGGAGTATGCTA
30240B_L	CTGAAATTTGCGGATCCAAC
30240B_R	GGCCGAGCAGATTAGTTGAG
30240C_L	ACGACTGAATGCAGGGCTAT
30240C_R	TGCGACTATGGATTCGTTCA
30240D_L	TTATCCATGGGCCAAAAATC
30240D_R	TAAGCTTTGTGGGCTTTGCT
30240E_L	AACATGAATCGGAGGTCAGC
30240E_R	TGTGTGATCATGGGCTGATT
M496L	CGAAGAATCCCGAACTCAAA
M496R	TAGGCTTGAATCAGGGCAAC
M496_2R	GCATCATACCCTCGATTCCG
FMitoF	CGAAGAATCCCGAACTCAAA
FMitoR	ATGGGTTTGGTGGGTCATTA

PCR reactions were done in 25 ul reactions of 1X Gold buffer (Perkin-Elmer, ABI), 0.2 mM of dNTPs, 2 mM $MgCl_2$, 0.4 mM of each primer, 0.8 mg/ml BSA (New England Biolabs) and (1 U of Taq Gold (Perkin-Elmer, ABI). Cycling conditions were 10 minutes at 95.0°C, and 35 cycles of 1 minute at 94.0°C, 1 minute at 50.0°C, and 1 minute at 72.0°C, with an extension of ten minutes at 72.0°C. PCR products were visualized on a 2% agarose gel and excess primers and dNTPs were removed by treatment with 1:10 dilution of ExoSAP-IT (Affymetrix) and six microliters of PCR products and heated to 37°C for 15 min and 85°C for 15 min. Cleaned PCR products were used for cycle sequencing using BigDye terminator premix version 3.1 (Applied Biosystems). Each reaction contained 0.7 µL Big Dye Terminator, 1.5 µl Big Dye Buffer, 5.5 µl PCR grade ddH2O, 0.3uM primer and 2 µl of PCR product. Cycling conditions were 2 minutes at

96.0°C, 25 cycles of 96.0°C for 10 seconds, 50.0°C for 10 seconds and 60.0°C for 4 minutes. Reactions were cleaned with Sephadex G-50 fine powder (GE Healthcare) and durapore membrane multiscreen filter plates (Millipore). Products were Sanger sequenced on an ABI 3130xl automated capillary sequencer and Geneious v7.0.6 was used to remove primers and align sequences. Eleven samples were Sanger sequenced (including samples with unambiguous base calls), two samples were thrown out for conflicting Sanger data but all other Sanger data clarified and confirmed our results.

Phylogeography

Haplotype diversity, nucleotide diversity and pairwise Fst were calculated in DNAsp v5.10.1 (Librado and Rozas 2009). We found a positive correlation between island area and the number of haplotypes recovered and haplotype diversity (Pearson's r=0.80 p-value=0.03 and r=0.77 p-value=0.04, respectively) (Figure S3). Number of haplotypes,

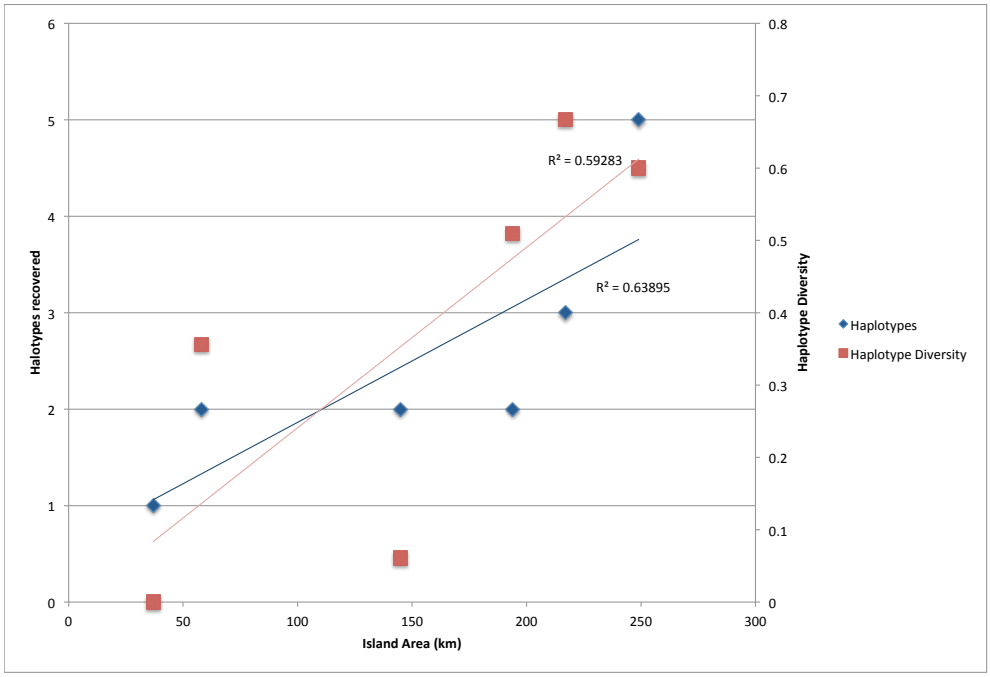


Figure S3 Haplotype and Haplotype Diversity Correlate with Island Area. A positive correlation was identified between island area and the number of haplotypes recovered and haplotype diversity (Pearson's r=0.80 p-value=0.03 and r=0.77 p-value=0.04, respectively).

haplotype diversity, and nucleotide diversity per island were not correlated with distance from the mainland or distance to the closest island with foxes (Table S5).

Table S5 Distances between Mainland and Islands

Locality	Distance from the mainland (km)[a]	Distance to next closest island with foxes (km)	Area (km^2)	2012 Estimated Population[b]
San Miguel	42	5	37	538
Santa Rosa	44	5	217	637
Santa Cruz	30	9	249	1354
Santa Catalina	32	34	194	1502
San Nicolas	98	77	58	No Estimate
San Clemente	79	34	145	795

[a]Physical characteristics based on Schoenherr et al. (1999:7).
[b]Estimates based spatially-explicit capture-recapture models and includes adults and pups (Island Fox Recovery Meeting 2013)

There was an east-west trend in the distribution of genetic variability across the northern islands, with the highest levels of variability in the east (Santa Cruz Island- five haplotypes) and the lowest in the west (San Miguel Island- one haplotype). Arelquin v3.5 was used to calculate the transitions and transversion found in each population (Excoffier and Lischer 2010).

Network analysis: Network analysis was conducted on an alignment stripped of monomorphic sites using the median joining algorithm as implemented in program Network v.4.612 using the default parameters (Anon 2014; Bandelt et al. 1999). Additional networks were generated for just the cytochrome b and d-loop regions (Figure S1). Analysis of cytochrome b (Figure S1B) suggests that a mainland northern California gray fox was introduced to Santa Catalina and later moved to San Clemente, to San Nicolas and to the Northern islands, potentially while the northern islands were connected in Santarosae as they share a single haplotype. The D-loop network (Figure S1B) does better that cytb in recovering unique haplotypes, but the region still on

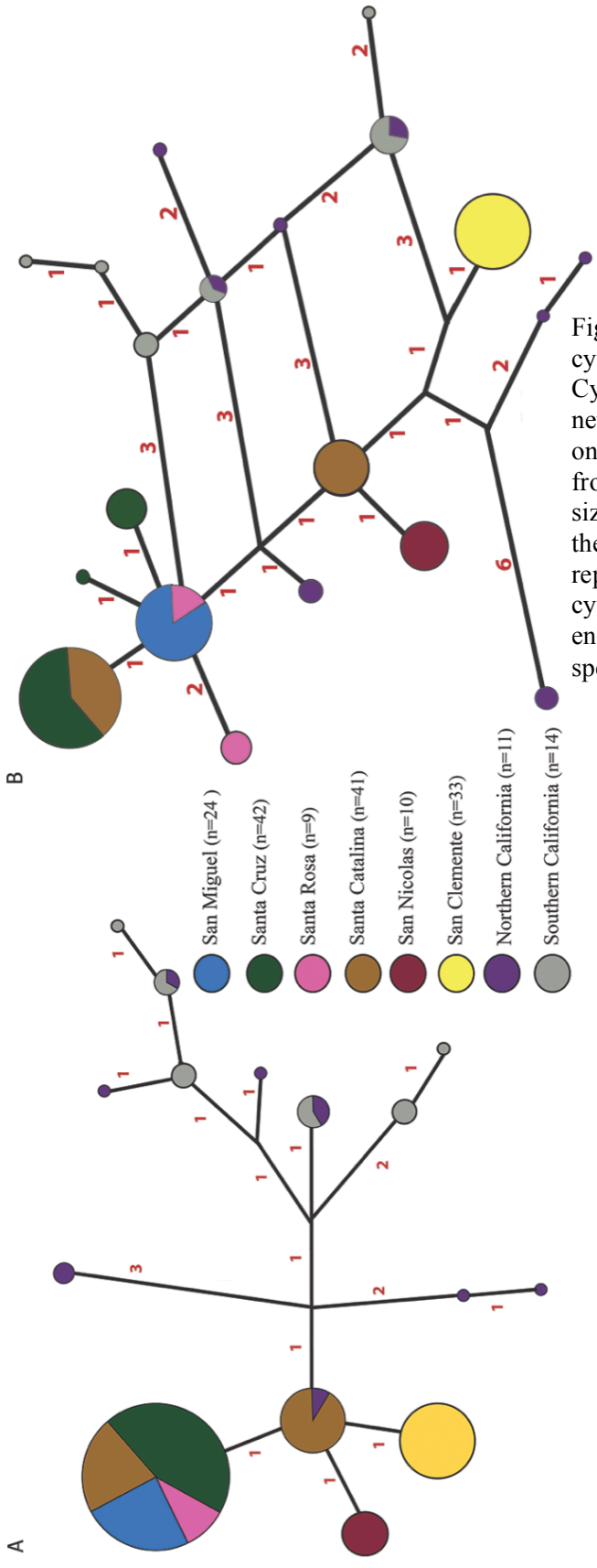


Figure S1. Network Analysis of cytochrome b and d-loop. Cytochrome b (1140 bp) only network (A) and d-loop (992 bp) only network (B) were generated from variable alignment sites. The size of the circles is proportional to the number of individuals represented by it. Neither cytochrome b nor d-loop had enough variants to detect all island-specific lineages.

recovers only 20 haplotypes. These networks suggest a very different population structure and evolutionary history than complete mitogenomes.

Selection analysis

To test for selection, an alignment of representative haplotypes was curated for coding genes only. As the mitogenome is a single unit of inheritance without recombination, the alignment was not partitioned in this analysis. Regions of genes with overlapping frames with another gene (ATP6/ATP8), were duplicated to allow for independent selection on overlapping codons. NADH6, which is coded on the opposite strand, was reverse complemented in the alignment to allow for a single reading frame across the coding genes. Stop codons were removed resulting in alignment of 11,286 bp. The HKY85 model was used for all subsequent selection analysis. We conducted selection analyses using six algorithms (SLAC, REL, FEL, IFEL, MEME, FUBAR) to test for mitogenome wide selection, codon specific selection and episodic diversifying selection (Kosakovsky Pond et al. 2006; Murrell et al. 2012, 2013; Pond et al. 2011; Pond and Frost 2005). Codon 258 in NADH1 was identified as under positive selection using FEL, IFEL, MEME and FUBAR, with p-values approaching significant in IFEL (0.07) and under 0.2 in FEL and MEME. The posterior probability for FUBAR was 0.855. PROVEAN v1.1.3 was used to determine if the changes in codon 258 affected chemical properties of the protein (Choi 2012; Choi et al. 2012). With a PROVEAN score of 0.096 (cutoff -2.5), this substitution is predicted to be neutral.

Phylogenetic analysis

To examine phylogenetic relationships between island, California and eastern gray foxes, additional publically available mammal mitochondrial genomes were obtained from GenBank and aligned to the fox dataset using Mafft v7.017 as implemented in Geneious 7.06 (Anon forthcoming; Katoh et al. 2002). The alignment was run through jModelTest v.2.1 and the GTR+I+G model was used to run 1000 pseudobootstrap replicates of the maximium likelihood tree program Garli (Figure S2) as implemented on the Lattice grid computing system (Bazinet et al. 2007; Bazinet and Cummings 2008, 2011; Cummings et al. 2003; Darriba et al. 2012; Zwickl 2006). We also conducted a parsimony analysis in PAUP* v4.0a131 that yielded the same topology as the maximum likelihood and Bayesian analyses.

To date the divergence between island and mainland foxes, Bayesian phylogenetic analysis was conducted in BEAST v.1.7.5 as implemented on the CIPRES web portal (Drummond et al. 2012; Drummond and Rambaut 2007; Miller et al. 2010). The eastern gray fox was used as an outgroup as indicated by the maximum likelihood analysis. Each gene was run through JModelTest v2.1 separately as well as the entire alignment and PartitionFinder v1.1.1 was used to test for codon partitioning. Based on this analysis, no codon partitioning and empirical base frequencies were used with each gene fitting the HKY or the TN93 model. We tested for a strict molecular clock in MEGA5 (Tamura et al. 2011) and equal evolutionary rates were rejected for both GTR and HKY models. However both a strict and a lognormal relaxed clock were used with a coalescent of constant size tree prior. The earliest radiocarbon date was used as a prior as the time to the most recent common ancestor for all island samples with a normal distribution around

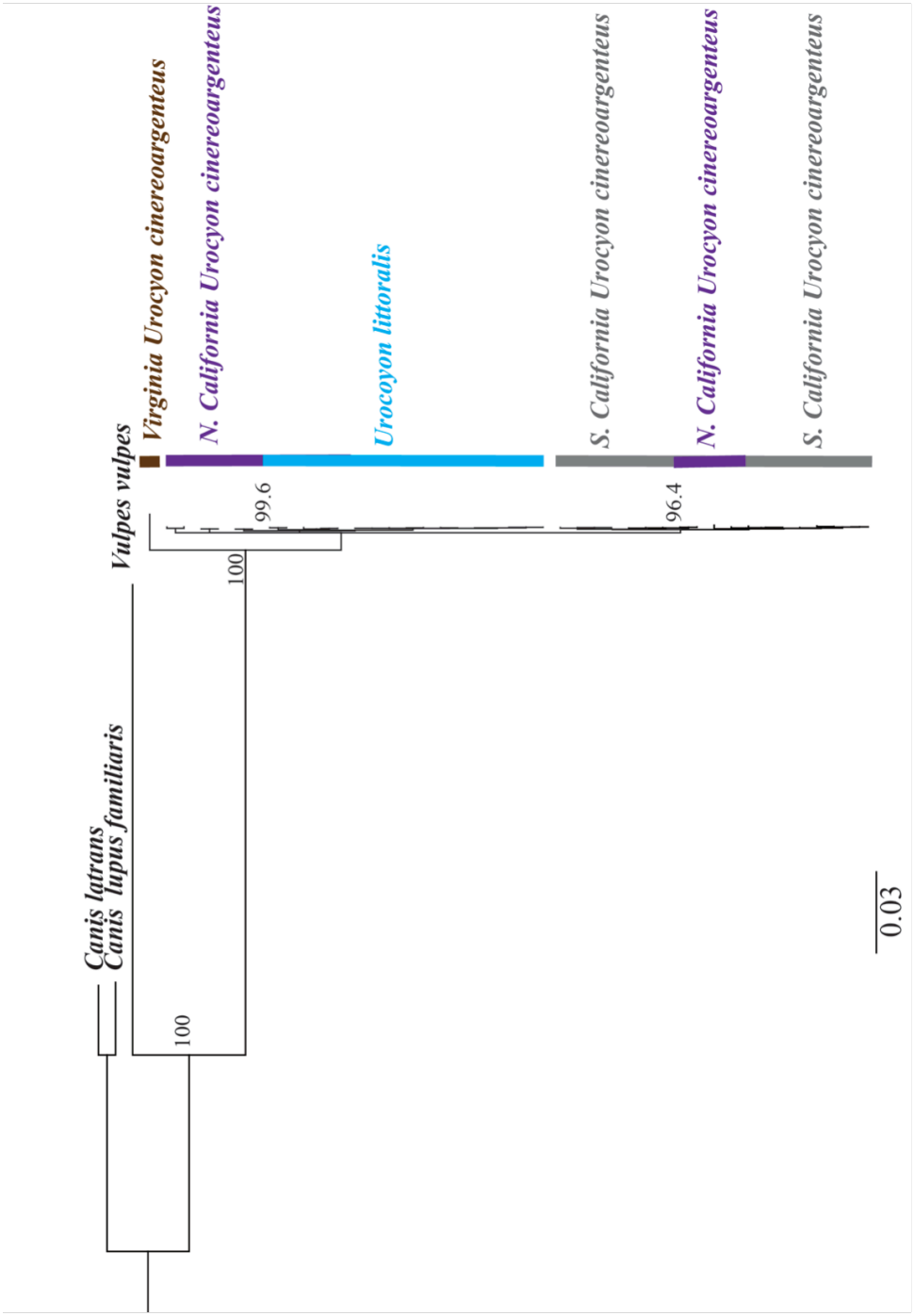


Figure S2. Maximum Likelihood Tree of Island and Gray Foxes. Rooted tree generated in Garli with 1000 bootstrap replicates. Key nodes are shown with bootstrap support. Nodes that are not labeled may also have strong support. Eastern gray fox is basal to the California clade and there is strong support for Clade A and Clade B (Figure 3).

the mean of 0.0070 (quantiles: median: 7E-3, 2.5% 5.04E-3, 97.5%: 8.96E-3) and standard deviation of 0.0010. The ucld.mean was changed to gamma distribution initial value 1, shape 0.0010, scale 1000 offset 0. As the eastern gray fox was the outgroup in this analysis, we set the tree model root length to the early Pliocene *Urocyon* fossil dating to 5.332-2.558 MYA (lognormal distribution 2.5% 0.273, median: 1.941, 97.5%: 13.78) (McKenna and Bell 1997). The root height was set with a lognormal distribution and initial value of 2.2, mean 3.2 with a log(stdev) of 1. All other priors were left to default settings and the MCMC was run in two independent runs of 100 million chains each, logging every 10,000 chains. The log files were examined in Tracer v1.6 to examine for convergence (Rambaut et al. 2013). An empty alignment was tested to sample for effects of the prior and the resulting poor posterior and prior ESS with values below 200 indicated that the priors were not strongly influencing the tree.

The mean substitution rate estimated in this analysis was 9.83% (95%HPD 5.557-14.52) per million years with a standard deviation of 2.35% and a median of 9.57% per million years for the run assuming a relaxed molecular clock. We compared this with the rates calculated from a strict molecular clock, which were 10 % per million years with a standard deviation of 2.35% and a median of 10% per million years. The strict clock was also tested even though the molecular clock test rejected, possibly as a result of serial bottlenecks in island foxes. Regardless, the rates are very similar, and do not effect the overall results of this analysis. We surveyed the literature for canid and mammal substitution rates and developed a database of rates for different taxa and markers (Bardeleben et al. 2005; Dalén et al. 2005; Edwards et al. 2012; Endicott and Ho 2008;

Freedman et al. 2014; Heller et al. 2012; Kutschera et al. 2013; Nabholz et al. 2008; Pang et al. 2009; Sacks and Louie 2008; Savolainen et al. 2002; Vila et al. 1999). Our estimated rates fall within canid substitution rates, which vary between markers, between taxa pairs and depending on which fossil calibration was used. Rates for human mitogenomes vary between 6.8 and 9.66 per site per million year depending on whether chimps are included or not included and in dog-wolf-coyotes between 0.64 and 1.92 per site per million year with an average of 3.3 per site per million years for mammals (Bardeleben et al. 2005; Dalén et al. 2005; Edwards et al. 2012; Endicott and Ho 2008; Freedman et al. 2014; Heller et al. 2012; Kutschera et al. 2013; Nabholz et al. 2008; Pang et al. 2009; Sacks and Louie 2008; Savolainen et al. 2002; Vila et al. 1999). The calculated substitution rate may be higher than expected due to the recent bottleneck due to a distemper outbreak in Channel Island foxes (Coonan et al. 2010). This could explain why the substitution rates are clustering beyond the average mitochondrial genome rates for a large dataset of mammals. Due to the distance between gray foxes and other canids, estimated to be greater than 10 million years (Lindblad-Toh et al. 2005), including an external calibration point is difficult when examining very shallow divergences. Comparison of small regions of the mitogenome to other canid datasets is not possible as there is not enough variation in these regions to resolve island fox biogeography. All of these issues lead to the elevated rate estimated and is a known problem in recent divergences (Ho et al. 2005, 2007).

Table S2. Distribution of polymorphisms in island and gray fox mitogenomes

		Noncoding	Coding				
	Property	**D-loop**	**CytB**	**rRNA**	**tRNA**	**All Coding Genes**	**Total**
	Length (bp)	992	1140	2547	1513	11356	16470
	Unvaried sites	965	1119	2533	1495	11133	16187
Island Only	Number of varied sites	11	3	3	6	51	68
	Proportion of varied sites	0.0111	0.0026	0.0012	0.0040	0.0045	0.0041
Mainland Only	Number of varied sites	21	18	11	12	175	219
	Proportion of varied sites	0.0212	0.0158	0.0043	0.0079	0.0154	0.0133
Island and Mainland	Number of varied sites	27	21	14	18	223	283
	Proportion of varied sites	0.0272	0.0184	0.0055	0.0119	0.0196	0.0172
	Transitions[a]	26	19	13	18	216	274
	Transversions[a]	1	2	1	0	9	11
	Transition/transversion ratio	26	9.5	13	-	24	24.91
	Haplotypes Recovered	20	15	13	16	33	35

[a] Calculated in Arlequin v.3.5

Table S1: Sample and Coverage Information

Sample ID	Location``	UTM Easting	UTM Northing	Collection	Tissue type	Extraction Kit	Library Prep Type	Platform	Lane	Mean Read Depth	Read Depth Std. Dev.	MtDNA Haplotype
MVZ-225021	Heggenberger Parkway Golf Course, Alameda	570630	4175095	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	66.61	23.5163	1
MVZ-225290	jct Harbor Bay Parkway and Ron Cowan Parkway, Alameda	568030	4175862	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	64.32	29.2356	1
MVZ-225670	22872 Walnut Blvd., Walnut Creek	584480	4194730	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	55.38	50.3052	3
MVZ-218726	Pinole Valley Rd. near Castro Ranch Rd., Pinole	565082	4203607	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	235.26	89.9407	4
MVZ-225294	Wldcat Canyon Road, just S Black Butte	553173	4582121	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	116.71	42.8173	5
9453C/120411	Catalina Island	368354	3694533	Santa Barbara Museum of Natural History	Tongue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	117.33	47.3183	30
48611	Catalina Island, East End	375993	3690332	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	3427.89	2250.56	31
49148	Catalina Island, East End	367290	3696489	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	5042.92	2769.8	30
51828	Catalina Island, West End	359824	3702581	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	4212.8	1635.43	31
51F0D	Catalina Island, East End	374297	3688024	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	4607.1	2889.04	31
52322	Catalina Island, East End	363233	3699211	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	4499.52	1926.41	30

53727	Catalina Island, East End	375339	3688471	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	5380.94	2332.61	31
53740	Catalina Island, West End	356996	3704475	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7316.77	882.234	30
58834	Catalina Island, West End	358482	3702357	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	5678.15	2174.25	30
59414	Catalina Island, East End	367176	3694989	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	1595.85	1395.2	30
61367	Catalina Island, West End	358833	3701255	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	2011.7	1944.71	30
62669	Catalina Island, West End	358485	3702613	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	2345.64	1901.61	31
63330	Catalina Island, West End	359503	3702350	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	3601.2	1949.5	31
63380	Catalina Island, West End	359864	3702167	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	1307.89	1504.71	31
63425	Catalina Island, East End	377525	3689600	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	1716.22	1634.61	30
71075	Catalina Island, East End	363466	3696922	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	6800.18	1183.22	31
74743	Catalina Island, West End	354918	3703133	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7861.92	507.962	30
78022	Catalina Island, East End	365222	3699331	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	2888.8	2008.79	30

80157	Catalina Island, East End	365968	3695742	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	6929.32	1132.73	30
85606	Catalina Island, West End	359643	3700359	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	69.0757	480.657	31
85661	Catalina Island, East End	371212	3692173	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	4733.57	2125.59	31
85871	Catalina Island, West End	353274	3703555	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	3248.91	2925.76	30
86740	Catalina Island, West End	356996	3704475	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	3879.08	3456.81	30
86765	Catalina Island, East End	374122	3690281	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	3758.87	1786.74	30
86784	Catalina Island, East End	361306	3701255	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	3039.88	1927.83	30
87067	Catalina Island, West End	359998	3702140	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	2376.5	1915.92	31
87682	Catalina Island, East End	370256	3694001	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	1084.94	1408.88	31
87785	Catalina Island, West End	355778	3704312	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	2852.75	1588.71	30
87970	Catalina Island, East End	368770	3696998	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	4685.53	1575.4	31
88196	Catalina Island, West End	359503	3702350	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	1634.84	1499.63	31

88351	Catalina Island, East End	376680	3687253	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	3017.61	1797.82	30
88406	Catalina Island, West End	359347	3702723	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	5928.68	1422.08	31
90186	Catalina Island, West End	356117	3704799	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7875.41	456.5	30
90302	Catalina Island, East End	365411	3695162	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	5832.92	1665.35	31
92421	Catalina Island, East End	363147	3695845	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	3568.63	3855.16	31
94745	Catalina Island, East End	366675	3691623	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7010.7	977.156	31
94867	Catalina Island, West End	353968	3704552	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7822.25	621.734	30
95091	Catalina Island, East End	368953	3695210	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	1735.29	1230.84	31
97686	Catalina Island, East End	368773	3692605	Catalina Island Conservancy	Blood clot	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7817.16	591.471	31
UNK22	Catalina Island	372011	3693095	Santa Barbara Museum of Natural History	Tongue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	140.52	48.2544	31
UNK23	Catalina Island	368354	3694533	Santa Barbara Museum of Natural History	Tongue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	154.89	50.228	31
985120029035544	San Clemente Island	350553	3654218	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1120.83	390.427	33
4451290268	San Clemente Island	351891	3654581	, Colorado State University, W. Chris Funk	Blood	Qiagen Blood-	Nextera style-	Illumina HiSeq	Lane 2	2523.52	947.248	33

						BioSprint	Capture					
985120027742591	San Clemente Island	357231.1979	3648401.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	201.066	64.2839	33
985120027742865	San Clemente Island	351171.1979	3654131.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7881.54	388.872	33
985120028532610	San Clemente Island	356301.1979	3642851.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	6272.4	2055.79	33
985120028546728	San Clemente Island	351891	3654581	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	5006.84	1791.85	33
985120028551893	San Clemente Island	356077	3643519	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1958.24	638.868	33
985120028845967	San Clemente Island	356541.1979	3644111.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7770.71	790.693	33
985120028866749	San Clemente Island	359751	3644651	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	3561.29	1426.61	33
985120028892352	San Clemente Island	363861	3638951	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	6506.04	1634.1	33
985120028919325	San Clemente Island	350541	3654941	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7886.36	356.804	33
985120029004811	San Clemente Island	356631	3648161	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	2046.23	985.227	33
985120029005330	San Clemente Island	355551.1979	3650171.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7865.8	449.059	33
985120030856620	San Clemente Island	359571.1979	3639071.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7885.4	385.475	32
985120030860616	San Clemente Island	355011.1979	3646481.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	3221.71	1419.21	33

985120030899238	San Clemente Island	362391.1979	3637511.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	85.8404	27.283	33
985120030920834	San Clemente Island	356751	3647351	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7878.75	391.087	33
985120030923763	San Clemente Island	362031.1979	3640241.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1174.54	392.522	33
985120031189688	San Clemente Island	356571.1979	3643601.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	4968.23	1904.79	33
985120031586905	San Clemente Island	356288.1258	3648385.698	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7653.22	763.475	33
985120032123337	San Clemente Island	353001.1979	3649361.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	5362.98	1619.35	33
985120032205152	San Clemente Island	356631	3648161	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7688.08	753.905	33
985120032253498	San Clemente Island	356391.1979	3645281.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	2298.45	833.817	33
985120032342258	San Clemente Island	352881.1979	3650681.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1592.07	555.123	33
985120032346926	San Clemente Island	355131.1979	3650741.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	5817.54	1903.74	33
985120032372226	San Clemente Island	352344.2787	3653793.885	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7804.06	586.673	33
985120032504581	San Clemente Island	352761.1979	3652001.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	6225.38	1611.52	33
985120032532213	San Clemente Island	360771.1979	3641381.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	33.6857	16.0528	33
430F762301	San Clemente Island	358041.1979	3642311.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	2639.16	717.947	33

454C113F32	San Clemente Island	351891	3654581	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7792.93	602.367	33
4A44416734	San Clemente Island	357921.1979	3646481.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7860.43	433.234	33
4A5867027B	San Clemente Island	359751	3644651	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	3839.99	127.15	33
4658713E74	San Clemente Island	360381.1979	3636941.225	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	985.542	325.384	33
MVZ-225303	Carmel Valley Road, just south of Carmel Valley Village	616886	4034993	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	143.94	80.0184	6
01PANT-20090525		11/427690	3725840	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	2068.05	607.405	12
01PEAN-20090302		11/427690	3725840	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1397.43	449.111	19
01PCLE-20090203		11/594494	3732687	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	2717.33	958.824	12
01PROB-20090109		11/594494	3732687	Colorado State University, W. Chris Funk	Blood	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1479.14	452.484	16
MVZ-225009	Fair Oaks region, Sacramento	650540	4279848	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	106.81	56.9379	7
F08		11/521481	3653528	Colorado State University, W. Chris Funk	Tongue	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	6989	1066.72	16
F11		11/521481	3653528	Colorado State University, W. Chris Funk	Tongue	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7306.63	1310.01	10
PWC-5206	East End of Santa Ynez Valley, Hwy 154 adj overlook just W of Cold Spring Bridge	239182	3824612	Santa Barbara Museum of Natural History	Muscle	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7891.7	207.384	18

PWC-5213	Hollister Ranch, access rd at jct Parcels 125 X 126	753372	3817693	Santa Barbara Museum of Natural History	Muscle	Qiagen Blood and Tissue Kit	Nextera style- Capture	Illumina HiSeq	Lane 2	7765.68	694.064	21
CHIS30121	San Miguel Island	745212	3769204	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7782.49	722.372	29
CHIS30361	San Miguel Island	744309	3769463	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7657.11	864.538	29
CHIS30415	San Miguel Island	744189	3769552	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7774.29	724.807	29
CHIS30091	San Miguel Island	744728	3769504	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7735.81	837.032	29
CHIS30061	San Miguel Island	742909	3770227	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	4804.53	1681.08	29
CHIS30399	San Miguel Island	745063	3769184	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	6535.43	1100.37	29
CHIS30373	San Miguel Island	744641	3769582	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7844	570.698	29
CHIS30459	San Miguel Island	744857	3769643	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7768.76	806.542	29
CHIS30388	San Miguel Island	744600	3769382	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	5350.13	1301.11	29
CHIS30118	San Miguel Island	744413	3769859	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7273.61	1067.55	29
CHIS30432	San Miguel Island	744330	3769867	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	282.14	151.513	29

CHIS30092	San Miguel Island	744365	3768890	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7867.1	487.685	29
CHIS30120	San Miguel Island	745348	3769299	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	7739.17	822.661	29
CHIS30417	San Miguel Island	745242	3769952	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	6771.27	1280.3	29
CHIS30413	San Miguel Island	745202	3769515	American Museum of Natural History	Blood	Qiagen Blood and Tissue Kit	Nextera style- Long Range PCR	Illumina HiSeq	Lane 1	5852.29	1388.28	29
CHIS 30358	San Miguel Island	746625	3768017	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	3050.61	942.643	29
CHIS 30362	San Miguel Island	743073	3768390	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	74.5681	24.4785	29
CHIS 30363	San Miguel Island	743073	3768390	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	132.425	42.5343	29
CHIS 30385	San Miguel Island	743073	3768390	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1332.06	506.412	29
CHIS 30392	San Miguel Island	746625	3768017	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	353.984	111.87	29
CHIS 30424	San Miguel Island	746625	3768017	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	91.8899	32.4108	29
CHIS 30441	San Miguel Island	746625	3768017	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1957.38	592.496	29
CHIS 30455	San Miguel Island	746625	3768017	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	122.705	39.5651	29
F118	Santa Cruz Island	251576	3764658	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1477.41	394.938	23
F128	Santa Cruz Island	263238	3768496	The Nature Conservancy	Blood	Qiagen Blood and	Nextera style-	Illumina HiSeq	Lane 2	7636.55	836.653	23

						Tissue Kit	Capture					
F248	Santa Cruz Island	260451	3766432	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7550.51	820.605	23
F333	Santa Cruz Island	249282	3765621	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7891.53	255.338	23
F345	Santa Cruz Island	241344	3768036	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7502.37	881.411	31
F351	Santa Cruz Island	254362	3766209	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	4510.24	1127.87	24
F400	Santa Cruz Island	238911	3765933	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7696.32	817.685	31
F419	Santa Cruz Island	263789	3768748	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7625.03	827.591	23
F435	Santa Cruz Island	252769	3765528	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7751.79	625.22	23
F438	Santa Cruz Island	244434	3763840	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	6926.05	1234.54	25
F441	Santa Cruz Island	249506	3765004	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	113.244	67.5294	23
F455	Santa Cruz Island	234103	3770620	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	5642.3	1475.64	25
F458	Santa Cruz Island	235893	3766001	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7875.76	254.521	25
M226	Santa Cruz Island	261430	3770226	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7632.98	983.112	23
M245	Santa Cruz Island	241716	3767298	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	5990.91	1484.01	23

M246	Santa Cruz Island	244230	3765828	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	3783.87	1037.55	23
M292	Santa Cruz Island	244067	3763681	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	5539.54	1538.43	23
M315	Santa Cruz Island	252932	3766690	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7832.71	476.22	23
M364	Santa Cruz Island	245391	3761692	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	3085.73	961.816	24
M409	Santa Cruz Island	231917	3773716	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7838.29	504.867	25
M434	Santa Cruz Island	263641	3766831	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	2756.84	891.341	23
M444	Santa Cruz Island	239914	3765981	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	2952.37	1011.89	31
M481	Santa Cruz Island	260451	3766432	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7448.16	952.397	23
M495	Santa Cruz Island	254680	3766524	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7898.22	204.217	23
M496	Santa Cruz Island	243700	3763522	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	4175.38	1095.58	22
M512	Santa Cruz Island	264045	3766843	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	3890.18	1107.42	23
M529	Santa Cruz Island	250500	3764612	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7630.14	843.027	23
M537	Santa Cruz Island	243837	3765905	The Nature Conservancy	Blood	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7771.23	507.818	23
F211	Santa Cruz Island	236129	3765611	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1457.32	417.262	25

F275	Santa Cruz Island	236646	3763944	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1072.49	322.489	25
F414	Santa Cruz Island	248789	3765253	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	4701.27	1411.9	23
F446	Santa Cruz Island	236837	3763881	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	7371.47	912.294	31
M178	Santa Cruz Island	236070	3766224	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	4195.68	1185.89	31
M418	Santa Cruz Island	252211	3765098	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	207.436	101.071	23
M425	Santa Cruz Island	236712	3763501	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1656.9	486.808	31
M429	Santa Cruz Island	235893	3766001	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	811.683	236.484	25
M459	Santa Cruz Island	252251	3764842	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	702.687	198.842	23
M465	Santa Cruz Island	252083	3764979	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	603.734	175.212	23
M497	Santa Cruz Island	248984	3765047	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1728.56	578.92	23
M511	Santa Cruz Island	236587	3763122	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	371.381	133.89	25
M561	Santa Cruz Island	248783	3764682	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1809.74	525.887	23
M562	Santa Cruz Island	248957	3764246	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	2786.65	878.635	23
CHIS 30240	Santa Rosa Island	759981	3761422	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	6512.9	1391.47	28

CHIS 30212	Santa Rosa Island	767592	3760504	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	4349.08	1281.73	27
CHIS 30244	Santa Rosa Island	767592	3760504	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1989.24	596.175	27
CHIS 30255	Santa Rosa Island	772826	3761070	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	754.097	227.353	26
CHIS 30298	Santa Rosa Island	772611	3761871	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	225.529	106.315	26
CHIS 30328	Santa Rosa Island	759981	3761422	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	2317.86	695.888	27
CHIS 30335	Santa Rosa Island	772826	3761070	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	330.34	103.171	26
CHIS 30343	Santa Rosa Island	772611	3761871	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	222.988	70.744	26
CHIS 30347	Santa Rosa Island	767592	3760504	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	250.266	79.5858	27
PWC-5219	Santa Ynez Valley, Brinkerhoff Rd, 1.5 mi N of Roblar Rd.	770877	3840812	Santa Barbara Museum of Natural History	Muscle	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	2591.42	831.623	14
PWC-5215	Santa Ynez Valley, Hwy 154	11/240028.78	3823888.76	Santa Barbara Museum of Natural History	Muscle	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7804.13	619.908	17
PWC-5218	Santa Ynez Valley, Hwy 154 0.3 mi W jct Paradise Rd.	11/237118	3825792	Santa Barbara Museum of Natural History	Muscle	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	594.53	224.545	20
PWC-5220	Santa Ynez Valley, Hwy 154, ~ 2 mi E of Cachuma Reservoir	11/239296	3824507	Santa Barbara Museum of Natural History	Muscle	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7539.72	954.037	13
PWC-5214	Santa Ynez Valley, Hwy 154, ~1.5 miles W Jct entrance to Cachuma county campground	11/225623	3830835	Santa Barbara Museum of Natural History	Muscle	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	7860.58	340.388	11

MVZ-206290	Hwy. 44, 0.25 mi W of Lassen Park Rd.	620249	4488911	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	171.66	51.659	5
MVZ-218693	15 Corte Dorado, Benicia	575094	4212822	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	200.41	91.68	8
MVZ-225297	Hwy 36 at Canyon View Road	604970	4466965	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	117.85	39.7729	2
MVZ-225296	Hwy 36 at Morgan Summit	624390	4469038	The Museum of Vertebrate Zoology at Berkeley	Tissue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	181.17	75.2111	9
PWC-5217	Hwy 33 near Foster Park	11/287643	3804254	Santa Barbara Museum of Natural History	Tissue	Qiagen Blood and Tissue Kit	Nextera style-Capture	Illumina HiSeq	Lane 2	3954.62	1655.74	15
4A590A0977	San Nicolas Island	261667.0029	3683448.004	Santa Barbara Museum of Natural History	Tongue	Qiagen Blood and Tissue Kit	454-Long Range PCR	454 Jr.	Run 1	532.88	189.258	35
4658582C6A	San Nicolas Island	261667.0029	3683448.004	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	2891.15	904.681	35
47237B1B0B	San Nicolas Island	268378.9973	3680792.008	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1213.58	340.127	35
472C575E42	San Nicolas Island	268378.9973	3680792.008	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	733.362	264.141	34
4947314B0B	San Nicolas Island	268378.9973	3680792.008	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	2140.64	725.618	35
49493E5D52	San Nicolas Island	261667.0029	3683448.004	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	968.068	320.046	35
4949A3D4D4C	San Nicolas Island	261667.0029	3683448.004	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	663.243	204.88	35
4A5A0A3248	San Nicolas Island	268378.9973	3680792.008	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1110.42	316.799	35
4B03640614	San Nicolas Island	268378.9973	3680792.008	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	1471.05	434.788	35

4B04785B14	San Nicolas Island	261667.0029	3683448.004	Colorado State University, W. Chris Funk	Blood clot	Qiagen Blood-BioSprint	Nextera style-Capture	Illumina HiSeq	Lane 2	3223.38	1048.15	35
CB17-1B Virginia	Woodstock, Virginia			CCEG Frozen Tissue Collection, Smithsonian Conservation Biology Institute			454-Long Range PCR	454 Jr.	Run 1	52.86	50.3052	36

Appendix B

Table S1: AMS Radiocarbon dates of island foxes

Locality		Collection	AMS Lab Number	δ13C ‰ VPDB	Conventional radiocarbon age, 14C yr BP ± 1 SD	cal yr BP age range (2 sigma)	Source
San Miguel Island	SMI-1	NHMLA	OxA-29849	-18.9	6307± 35	7310-7170	This Paper
	Locality V-7c	SBMNH	UCIAMS-40173	−17.0	6120 ± 25	7160-6910	Rick et al 2009
	SMI-261	NHLMA	OxA-29773	-16.8	1034± 24	980-920	This Paper
	Locality V-10c	SBMNH	UCIAMS-38253	−18.4	990 ± 15	950–800	Rick et al 2009
	SMI-261	NHLMA	OxA-29848	-17	990 ± 24	960-800	This Paper
	Locality V-11	SBMNH	UCIAMS-38252	−19.5	220 ± 15	300–0	Rick et al 2009
Santa Rosa Island	SRI-41	SBMNH	OxA-29779	-18.6	3469 ± 28	3830-3640	This Paper
	Upper Tecolote Member	SBMNH	UCR-3563	n/a	1440 ± 50	1510-1280	Shelley 2001
	SRI-1	SBMNH	OxA-29851	-17.3	1294 ± 25	1290-1180	This Paper
	SRI-4	SBMNH	OxA-29778	-19	632 ± 24	660-550	This Paper
	SRI-2	SBMNH	OxA-29776	-18.6	443 ± 24	530-480	This Paper
	SRI-1	SBMNH	OxA-29850	-15.7	344 ± 24	480-320	This Paper
	SRI-3	SBMNH	OxA-29777	-18.8	216 ± 23	310-0	This Paper
Santa Cruz Island	SCRI-333	UCSB-Repository	OxA-29196	-17.38	5290 ± 30	6180-5955	This Paper
	SCRI-333	UCSB-Repository	OxA-29197	-18.21	2553 ± 26	2750-2510	This Paper
Anacapa Island	ANI-2		OxA-30069	-16.76	2956 ± 27	3210-3010	This Paper

Santa Catalina Island	SCAI-17 Pit7	Catalina Island Museum	OxA-27377	-17.64	4636 ±28	5460-5310	This Paper
San Nicolas Island	SNI-11	SBMNH	Beta 106185	n/a	4940 ± 50	5070-4790*	Shelley 2001
	SNI-16	CalState-LA	OxA-29075	-17.6	1859 ± 24	1870-1730	This Paper
	SNI-25-South Locus	CalState-LA	OxA-29198	-17.36	447 ± 21	530-490	This Paper
	SNI-25-East Locus	CalState-LA	OxA-29074	-17.11	366 ± 22	500-320	This Paper
San Clemente Island	SCLI-43C	CalState-Northridge	Beta 106185	n/a	2110 ±50	2200-2300	Shelley 2001
	SCLI-43	CalState-Northridge	OxA-29073	-17.48	1772 ± 24	1810-1610	This Paper
	SCLI-1524	CalState-Northridge	OxA-29166	-20	486 ± 24	540-500	This Paper
	SCLI-1531	CalState-Northridge	OxA-29195	-17.75	449 ± 22	530-490	This Paper
	SCLI-1524	CalState-Northridge	OxA-29070	-18.3	260 ± 25	430-150	This Paper
	SCLI-1524	CalState-Northridge	OxA-29071	-18.5	207 ± 24	300-0	This Paper

*Indicates marine calibration using the Marine13 calibration curve and a local marine correction (delta-R) of 261± 21.
One date reported in Hofman et al. 2015 was removed because analyses determined that it was not a fox.

Table S2 : Isotope and Sample Data

Sample ID	Sex	$\delta^{13}C$	$\delta^{13}C$ Seuss	$\delta^{15}N$	Species	Year	Island
SBMNH OS 1497	Male	-15.3	-14.86	7.9	Gray Fox	1977	Mainland
SBMNH OS 1530	Male	-10.6	-10.12	14.1	Gray Fox	1978	Mainland
SBMNH MAM 1953	male	-16.5	-16.04	8.3	Gray Fox	1979	Mainland
SBMNH MAM 1949	female	-15.9	-15.44	7.8	Gray Fox	1979	Mainland
SBMNH MAM 2021	male	-20.5	-19.84	7.6	Gray Fox	1980	Mainland
SBMNH MAM 2020	male	-20.4	-19.78	6.2	Gray Fox	1980	Mainland
SBMNH MAM 2056	male	-19.4	-18.73	6.3	Gray Fox	1980	Mainland
SBMNH MAM 2165	male	-21.2	-20.58	5.1	Gray Fox	1981	Mainland
SBMNH OS 3677	male	-21.8	-21.14	7.8	Gray Fox	1982	Mainland
SBMNH MAM 2109	female	-21.1	-20.48	7.9	Gray Fox	1982	Mainland
SBMNH OS 3130	male	-18.9	-18.21	5.2	Gray Fox	1984	Mainland
SBMNH OS 3131	male	-18.6	-17.90	5.7	Gray Fox	1984	Mainland
SBMNH OS 3986	male	-17.9	-17.29	2.4	Gray Fox	1985	Mainland
SBMNH MAM 2950	male	-21.8	-21.09	7.6	Gray Fox	1987	Mainland
SBMNH OS 3988	female	-21.1	-20.44	9.8	Gray Fox	1987	Mainland
SBMNH OS 3902	female	-21.0	-20.36	8.6	Gray Fox	1987	Mainland
SBMNH MAM 2942	male	-21.7	-21.06	7.7	Gray Fox	1989	Mainland
SBMNH MAM 3099	male	-21.2	-20.53	6.4	Gray Fox	1989	Mainland
SBMNH MAM 2924	male	-18.6	-17.95	9.9	Gray Fox	1989	Mainland
SBMNH MAM 3090	female	-19.3	-18.43	6.2	Gray Fox	1990	Mainland
SBMNH MAM 3092	male	-21.1	-20.22	4.8	Gray Fox	1993	Mainland
SBMNH MAM 3091	female	-18.0	-17.15	4.8	Gray Fox	1993	Mainland
SBMNH MAM 4053	male	-21.8	-20.70	6.7	Gray Fox	2003	Mainland
SBMNH MAM 9001	male	-19.7	-18.61	5.3	Gray Fox	2005	Mainland
USNM 12269	female	-18.6	-18.57	11.8	Island Fox	1863	San Clemente
USNM 18279	unknown	-19.0	-18.88	9.1	Island	1889	San

					Fox		Clemente
USNM 60673	female	-20.0	-19.77	10.0	Island Fox	1894	San Clemente
USNM 61368	female	-18.5	-18.31	13.2	Island Fox	1894	San Clemente
USNM 60674	female	-13.2	-13.00	13.6	Island Fox	1894	San Clemente
USNM 92030	female	-18.6	-18.39	11.3	Island Fox	1897	San Clemente
USNM 92033	male	-18.4	-18.17	14.0	Island Fox	1897	San Clemente
USNM 92031	female	-18.2	-18.05	14.4	Island Fox	1897	San Clemente
USNM 92032	female	-16.3	-16.11	14.3	Island Fox	1897	San Clemente
USNM 92029	male	-14.7	-14.49	14.9	Island Fox	1897	San Clemente
SBMNH OS 836	female	-18.6	-18.20	13.6	Island Fox	1972	San Clemente
SBMNH OS 1593	unknown	-14.8	-14.37	16.3	Island Fox	1977	San Clemente
SBMNH OS 2442	unknown	-17.4	-16.76	14.3	Island Fox	1981	San Clemente
SBMNH MAM 2112	male	-17.0	-16.39	13.6	Island Fox	1981	San Clemente
SBMNH OS 2981	female	-15.9	-15.28	13.4	Island Fox	1981	San Clemente
SBMNH MAM 2046	male	-15.8	-15.14	12.2	Island Fox	1981	San Clemente
SBMNH OS 2547	male	-19.4	-18.73	13.0	Island Fox	1982	San Clemente
SBMNH OS 2627	male	-18.5	-17.82	10.9	Island Fox	1982	San Clemente
SBMNH OS 2980	male	-16.5	-15.85	10.5	Island Fox	1982	San Clemente
SBMNH MAM 2082	male	-15.7	-15.08	14.8	Island Fox	1982	San Clemente
SBMNH OS 3435	female	-15.5	-14.80	13.5	Island Fox	1982	San Clemente
SBMNH MAM 2080	male	-15.2	-14.56	15.3	Island Fox	1982	San Clemente
SBMNH OS 2548	male	-15.2	-14.50	12.5	Island Fox	1982	San Clemente
SBMNH MAM 2164	male	-13.0	-12.38	13.3	Island Fox	1982	San Clemente
SBMNH OS 3132	male	-16.4	-15.75	13.8	Island Fox	1983	San Clemente
CalState-NR SCLI-1524 13S-15E	unknown	-20.6	-20.59	13.2	Island Fox	Late Holocene	San Clemente
CalState-NR SCLI-1524 7S-15E	unknown	-19.3	-19.29	16.9	Island Fox	Late Holocene	San Clemente
CalState-NR SCLI-1524 7S-	unknown	-19.2	-19.15	16.6	Island Fox	Late Holoce	San Clemente

15E						ne	
CalState-NR SCLI-1531/LT-11 92 5S-1E	unknown	-18.3	-18.25	15.6	Island Fox	Late Holocene	San Clemente
CalState-NR SCLI-43 30N-14E 03406	unknown	-17.5	-17.55	12.2	Island Fox	Late Holocene	San Clemente
CalState-NR SCLI-1524 9S-17E F4	unknown	-14.4	-14.45	19.2	Dog	Late Holocene	San Clemente
USNM 34845	female	-20.5	-20.30	9.9	Island Fox	1892	San Miguel
USNM 34846	female	-20.1	-19.92	9.1	Island Fox	1892	San Miguel
SBMNH OS 1377	unknown	-17.8	-17.32	9.3	Island Fox	1975	San Miguel
SBMNH OS 926	male	-18.6	-18.17	8.4	Island Fox	1976	San Miguel
SBMNH OS 925	unknown	-18.5	-18.01	8.5	Island Fox	1976	San Miguel
SBMNH OS 1201	male	-19.1	-18.70	8.1	Island Fox	1977	San Miguel
SBMNH OS 1737	female	-18.7	-18.30	7.6	Island Fox	1977	San Miguel
SBMNH OS 1256	unknown	-18.6	-18.17	9.2	Island Fox	1977	San Miguel
SBMNH MAM 8977	unknown	-18.5	-18.01	7.7	Island Fox	1977	San Miguel
SBMNH OS 1255	male	-18.2	-17.80	8.7	Island Fox	1977	San Miguel
SBMNH OS 1257	male	-17.9	-17.45	10.5	Island Fox	1977	San Miguel
SBMNH OS 1547	unknown	-19.4	-18.97	10.7	Island Fox	1978	San Miguel
SBMNH OS 1641	unknown	-19.0	-18.52	6.9	Island Fox	1978	San Miguel
SBMNH OS 1677	unknown	-18.3	-17.85	8.2	Island Fox	1978	San Miguel
SBMNH OS 1602	unknown	-18.2	-17.74	10.2	Island Fox	1978	San Miguel
SBMNH OS 1549	unknown	-17.4	-16.93	9.9	Island Fox	1978	San Miguel
SBMNH OS 1548	unknown	-15.6	-15.19	12.9	Island Fox	1978	San Miguel
SBMNH MAM 2022	female	-19.0	-18.54	8.6	Island Fox	1979	San Miguel
SBMNH OS 1795	male	-18.4	-18.00	9.8	Island Fox	1979	San Miguel
SBMNH OS 1796	male	-17.8	-17.33	12.8	Island Fox	1979	San Miguel
SBMNH OS 2138	unknown	-20.0	-19.34	7.7	Island Fox	1980	San Miguel
SBMNH OS 2644	unknown	-17.5	-16.81	9.0	Island Fox	1982	San Miguel

SBMNH MAM 4326	unknown	-18.9	-18.21	7.7	Island Fox	1984	San Miguel
SBMNH OS 3424	female	-19.5	-18.84	7.0	Island Fox	1985	San Miguel
SBMNH MAM 3193	female	-18.6	-17.93	8.3	Island Fox	1986	San Miguel
SBMNH MAM 4325	unknown	-18.6	-17.96	10.1	Island Fox	1988	San Miguel
SBMNH OS 4882	unknown	-19.3	-18.38	9.2	Island Fox	1996	San Miguel
SBMNH OS 4887	male	-19.2	-18.35	8.9	Island Fox	1996	San Miguel
SBMNH OS 4886	unknown	-18.2	-17.35	11.9	Island Fox	1996	San Miguel
NHMLA SMI-1 A.6431.6940	unknown	-18.9	-18.90	8.0	Island Fox	Early Holocene	San Miguel
SBMNH OS 1259	unknown	-17.9	-17.50	9.5	Island Fox	Historic	San Miguel
USNM 14381	unknown	-20.0	-19.55	10.8	Island Fox	Historic	San Miguel
USNM 1417	unknown	-18.6	-18.06	10.1	Island Fox	Historic	San Miguel
NHMLA SMI-261 A.6431.64.5799	unknown	-17.0	-17.00	11.2	Island Fox	Late Holocene	San Miguel
NHMLA SMI-261 A.6431.64.5836	unknown	-16.8	-16.80	12.5	Island Fox	Late Holocene	San Miguel
USNM 307394	male	-20.1	-19.72	10.8	Island Fox	1940	San Nicolas
USNM 307393	female	-19.8	-19.44	7.9	Island Fox	1940	San Nicolas
SBMNH OS 1814	unknown	-19.3	-18.90	6.3	Island Fox	1974	San Nicolas
SBMNH OS 1818	unknown	-18.2	-17.75	7.6	Island Fox	1974	San Nicolas
SBMNH OS 1074	female	-17.3	-16.89	7.7	Island Fox	1976	San Nicolas
SBMNH OS 2081	unknown	-19.5	-19.02	6.7	Island Fox	1977	San Nicolas
SBMNH MAM 2061	male	-21.3	-20.59	11.3	Island Fox	1982	San Nicolas
SBMNH OS 3431	female	-18.4	-17.70	8.7	Island Fox	1982	San Nicolas
SBMNH OS 3137	unknown	-19.5	-18.79	6.7	Island Fox	1984	San Nicolas
SBMNH OS 3434	female	-19.3	-18.64	7.6	Island Fox	1984	San Nicolas
SBMNH OS 3135	male	-18.5	-17.81	7.6	Island Fox	1984	San Nicolas
SBMNH OS 3270	female	-15.1	-14.46	13.4	Island Fox	1984	San Nicolas
SBMNH OS 3707	male	-19.9	-19.19	8.6	Island Fox	1985	San Nicolas

SBMNH MAM 2322	female	-19.0	-18.29	9.0	Island Fox	1985	San Nicolas
SBMNH OS 3678	male	-18.4	-17.72	11.7	Island Fox	1985	San Nicolas
SBMNH OS 3281	female	-18.2	-17.51	8.3	Island Fox	1985	San Nicolas
SBMNH OS 3710	male	-16.2	-15.51	10.9	Island Fox	1985	San Nicolas
SBMNH OS 3706	female	-19.3	-18.63	11.6	Island Fox	1986	San Nicolas
SBMNH OS 3711	male	-17.5	-16.84	10.8	Island Fox	1986	San Nicolas
SBMNH MAM 2954	male	-18.4	-17.71	10.3	Island Fox	1987	San Nicolas
SBMNH MAM 2974	female	-17.2	-16.57	14.0	Island Fox	1987	San Nicolas
SBMNH MAM 2956	female	-17.2	-16.51	11.2	Island Fox	1987	San Nicolas
SBMNH MAM 2953	male	-16.9	-16.26	12.5	Island Fox	1987	San Nicolas
SBMNH OS 4883	unknown	-18.9	-18.03	7.6	Island Fox	1990	San Nicolas
SBMNH OS 4860	unknown	-16.0	-15.10	12.7	Island Fox	1993	San Nicolas
SBMNH OS 5151	male	-22.0	-21.08	6.8	Island Fox	1995	San Nicolas
SBMNH OS 4993	unknown	-18.5	-17.61	10.3	Island Fox	1999	San Nicolas
USNM 38201	unknown	-11.7	-11.18	16.1	Island Fox	Historic	San Nicolas
SBMNH OS SNI-7 2994	female	-16.4	-16.36	14.1	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2986	female	-15.7	-15.66	14.5	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2993	unknown	-15.4	-15.45	15.0	Island Fox	Late Holocene	San Nicolas
CalState-LA SNI-16	unknown	-18.4	-18.40	11.3	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2992	male	-17.5	-17.47	12.7	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2991	male	-16.7	-16.65	11.4	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2987	male	-16.4	-16.42	13.8	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2990	female	-15.6	-15.61	13.8	Island Fox	Late Holocene	San Nicolas
SNI-7 Island	unknown	-15.2	-15.23	16.1	Island	Late	San Nicolas

Fox SNI-7					Fox	Holocene	
CalState-LA SNI-25-SouthLocus	unknown	-17.9	-17.90	12.6	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2989	male	-17.3	-17.30	14.3	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2985	female	-16.8	-16.83	12.7	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2995	unknown	-16.8	-16.76	11.5	Island Fox	Late Holocene	San Nicolas
SNI-25 Island Fox SNI-25	unknown	-16.7	-16.70	15.7	Island Fox	Late Holocene	San Nicolas
CalState-LA SNI-25-East Locus	unknown	-16.7	-16.65	16.4	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2984	female	-16.5	-16.50	13.1	Island Fox	Late Holocene	San Nicolas
SBMNH OS SNI-7 2988	male	-14.4	-14.37	17.4	Island Fox	Late Holocene	San Nicolas
USNM 15663	unknown	-20.7	-20.61	9.4	Island Fox	1875	Santa Catalina
USNM 188079	male	-22.3	-22.17	10.3	Island Fox	1885	Santa Catalina
USNM 188078	male	-22.9	-22.72	10.0	Island Fox	1886	Santa Catalina
USNM 188087	male	-22.4	-22.25	8.7	Island Fox	1886	Santa Catalina
USNM 188083	female	-21.1	-20.92	8.8	Island Fox	1886	Santa Catalina
USNM 188082	female	-20.5	-20.31	7.6	Island Fox	1886	Santa Catalina
USNM 188081	female	-19.6	-19.48	9.4	Island Fox	1886	Santa Catalina
USNM 188086	male	-19.3	-19.18	9.5	Island Fox	1886	Santa Catalina
USNM 188085	male	-18.9	-18.75	7.6	Island Fox	1886	Santa Catalina
USNM 188080	female	-18.8	-18.70	7.7	Island Fox	1886	Santa Catalina
USNM 188084	male	-18.6	-18.42	8.0	Island Fox	1886	Santa Catalina
SBMNH MAM 1540	male	-18.9	-18.48	8.2	Island Fox	1977	Santa Catalina
SBMNH MAM 1918	male	-20.0	-19.52	8.3	Island Fox	1979	Santa Catalina
SBMNH OS 2131	male	-19.4	-18.94	8.4	Island Fox	1979	Santa Catalina

SBMNH MAM 2180	male	-19.2	-18.49	7.9	Island Fox	1983	Santa Catalina
SBMNH OS 3136	male	-18.8	-18.16	8.8	Island Fox	1984	Santa Catalina
SBMNH MAM 2328	male	-18.6	-17.96	7.5	Island Fox	1984	Santa Catalina
SBMNH MAM 2324	male	-17.2	-16.52	10.7	Island Fox	1984	Santa Catalina
SBMNH MAM 2941	male	-18.3	-17.68	8.3	Island Fox	1988	Santa Catalina
USNM 33224	female	-19.2	-19.02	9.2	Island Fox	Historic	Santa Catalina
Catalina Island Museum SCAI-17 Pit 7	unknown	-19.0	-18.97	9.6	Island Fox	Middle Holocene	Santa Catalina
USNM 12548	male	-19.3	-19.23	7.9	Island Fox	1875	Santa Cruz
USNM 34854	unknown	-20.2	-20.04	10.4	Island Fox	1892	Santa Cruz
USNM 34853	male	-20.2	-20.00	9.9	Island Fox	1892	Santa Cruz
SBMNH OS 7	unknown	-19.3	-18.95	10.0	Island Fox	1927	Santa Cruz
SBMNH OS 6	unknown	-19.0	-18.68	11.0	Island Fox	1927	Santa Cruz
SBMNH OS 9	unknown	-18.9	-18.64	8.3	Island Fox	1927	Santa Cruz
SBMNH OS 8	unknown	-18.9	-18.61	10.8	Island Fox	1927	Santa Cruz
SBMNH OS 179	unknown	-18.8	-18.54	10.3	Island Fox	1927	Santa Cruz
SBMNH OS 178	female	-17.9	-17.60	8.9	Island Fox	1927	Santa Cruz
SBMNH OS 2364	unknown	-19.7	-19.24	6.9	Island Fox	1979	Santa Cruz
SBMNH OS 2366	unknown	-19.6	-19.13	9.8	Island Fox	1979	Santa Cruz
SBMNH OS 2367	unknown	-19.0	-18.56	6.9	Island Fox	1979	Santa Cruz
SBMNH OS 2369	unknown	-18.8	-18.41	10.4	Island Fox	1979	Santa Cruz
SBMNH OS 2368	unknown	-18.8	-18.39	7.5	Island Fox	1979	Santa Cruz
SBMNH OS 2363	unknown	-18.2	-17.72	10.6	Island Fox	1979	Santa Cruz
SBMNH OS 2362	male	-18.0	-17.54	9.4	Island Fox	1979	Santa Cruz
SBMNH OS 2063	female	-19.5	-18.86	8.6	Island Fox	1980	Santa Cruz
SBMNH MAM 2002	male	-19.6	-18.98	8.3	Island Fox	Historic	Santa Cruz
SBMNH Anthro SCRI-496 NA-CA-SCRI-XX13C-5	unknown	-21.1	-21.13	7.6	Island Fox	Late Holocene	Santa Cruz

SBMNH Anth SCRI-1 SCRI-64		-19.9	-19.90	6.0	Island Fox	Late Holocene	Santa Cruz
SBMNH Anthro SCRI-257 site 3 # 6	unknown	-19.6	-19.62	8.0	Island Fox	Late Holocene	Santa Cruz
SBMNH Anthro SCRI-257 site 3 # 5	unknown	-19.4	-19.38	6.4	Island Fox	Late Holocene	Santa Cruz
SBMNH Anthro SCRI-257 site 3 #1	unknown	-19.1	-19.15	8.0	Island Fox	Late Holocene	Santa Cruz
UCSB SCRI-333 6A Central	unknown	-19.0	-19.01	7.7	Island Fox	Late Holocene	Santa Cruz
SBMNH Anthro SCRI-496 NA-CA SCRI-XX13C-4	unknown	-19.0	-18.99	9.2	Island Fox	Late Holocene	Santa Cruz
SBMNH Anthro SCRI-257 site 3 # 8	unknown	-18.9	-18.85	7.0	Island Fox	Late Holocene	Santa Cruz
SBMNH Anthro SCRI-1 NA-SCRI-1-63	unknown	-18.5	-18.52	8.1	Island Fox	Late Holocene	Santa Cruz
UCSB SCRI-333 11B Central	unknown	-17.7	-17.72	10.3	Island Fox	Middle Holocene	Santa Cruz
USNM 18278	unknown	-18.9	-18.79	10.2	Island Fox	1889	Santa Rosa
USNM 34849	male	-20.8	-20.64	9.7	Island Fox	1892	Santa Rosa
USNM 34851	male	-20.6	-20.35	8.8	Island Fox	1892	Santa Rosa
USNM 34848	male	-20.5	-20.25	10.3	Island Fox	1892	Santa Rosa
USNM 34847	male	-19.0	-18.85	14.7	Island Fox	1892	Santa Rosa
USNM 34850	male	-17.0	-16.83	14.4	Island Fox	1892	Santa Rosa
SBMNH OS 3	unknown	-19.7	-19.41	8.8	Island Fox	1929	Santa Rosa
SBMNH OS 4	unknown	-19.5	-19.20	9.7	Island Fox	1929	Santa Rosa
USNM 307395	male	-19.4	-18.99	9.3	Island Fox	1941	Santa Rosa
USNM 307396	female	-13.7	-13.26	12.8	Island Fox	1941	Santa Rosa
SBMNH OS 1258	male	-19.6	-19.11	11.4	Island Fox	1970	Santa Rosa
SBMNH OS 872	female	-19.7	-19.22	9.3	Island Fox	1975	Santa Rosa
SBMNH OS 870	female	-19.4	-18.94	11.1	Island Fox	1975	Santa Rosa
SBMNH OS 871	male	-17.6	-17.15	10.0	Island	1975	Santa Rosa

					Fox		
SBMNH OS 927	male	-18.3	-17.84	9.4	Island Fox	1976	Santa Rosa
SBMNH OS 928	male	-16.9	-16.46	10.8	Island Fox	1976	Santa Rosa
SBMNH OS 1202	female	-19.2	-18.71	11.0	Island Fox	1977	Santa Rosa
SBMNH OS 3182	female	-20.6	-19.93	10.2	Island Fox	1984	Santa Rosa
SBMNH OS 3439	male	-17.4	-16.70	11.4	Island Fox	1986	Santa Rosa
SBMNH OS 3811	female	-20.3	-19.66	11.0	Island Fox	1988	Santa Rosa
SBMNH OS 3753	male	-20.3	-19.64	10.8	Island Fox	1988	Santa Rosa
SBMNH OS 3705	female	-16.8	-16.13	12.0	Island Fox	1988	Santa Rosa
SBMNH MAM 3089	male	-20.5	-19.64	11.8	Island Fox	1993	Santa Rosa
SBMNH OS 4748	unknown	-19.3	-18.47	10.6	Island Fox	1994	Santa Rosa
SBMNH Anth SRI-X SRI 44.1-A		-19.5	-19.50	8.3	Island Fox	Late Holocene	Santa Rosa
SBMNH Anthro SRI-670 CHIS-12741	unknown	-19.3	-19.33	7.9	Island Fox	Late Holocene	Santa Rosa
SBMNH Anthro SRI 168 NA-CA-SRI-168.1	unknown	-19.1	-19.14	6.8	Island Fox	Late Holocene	Santa Rosa
SBMNH Anthro SRI-2A 3944	unknown	-19.0	-19.03	8.5	Island Fox	Late Holocene	Santa Rosa
SBMNH OS SRI-3 844	unknown	-18.8	-18.80	9.9	Island Fox	Late Holocene	Santa Rosa
SBMNH Anthro SRI-670 CHIS-13007	unknown	-18.6	-18.62	11.8	Island Fox	Late Holocene	Santa Rosa
SBMNH OS 217	unknown	-18.6	-18.62	8.9	Island Fox	Late Holocene	Santa Rosa
SBMNH OS SRI-2 2692	unknown	-18.6	-18.60	8.0	Island Fox	Late Holocene	Santa Rosa
SBMNH OS SRI-4 838	unknown	-18.6	-18.60	9.3	Island Fox	Late Holocene	Santa Rosa
SBMNH OS 860	unknown	-18.6	-18.58	11.6	Island Fox	Late Holocene	Santa Rosa
SBMNH Anth SRI-X SRI 44.1-B		-18.3	-18.33	9.5	Island Fox	Late Holocene	Santa Rosa
SBMNH OS 990	unknown	-17.7	-17.68	10.4	Island	Late	Santa Rosa

					Fox	Holocene	
SBMNH Anth SRI-X SRI 44.2		-17.6	-17.63	10.1	Island Fox	Late Holocene	Santa Rosa
SBMNH OS 850	unknown	-17.6	-17.61	10.2	Island Fox	Late Holocene	Santa Rosa
SBMNH OS SRI-1 861	unknown	-17.4	-17.41	11.5	Island Fox	Late Holocene	Santa Rosa
SBMNH OS SRI-1 862	unknown	-17.3	-17.30	11.1	Island Fox	Late Holocene	Santa Rosa
SBMNH OS SRI-3 845	unknown	-17.2	-17.22	10.9	Island Fox	Late Holocene	Santa Rosa
SBMNH OS 835	unknown	-16.2	-16.16	12.7	Island Fox	Late Holocene	Santa Rosa
SBMNH OS Upper Tecolote 2327	female	-15.8	-15.78	14.3	Island Fox	Late Holocene	Santa Rosa
SBMNH OS SRI-41 846	unknown	-18.6	-18.60	8.8	Island Fox	Middle Holocene	Santa Rosa
ANI-2	unknown	-16.8	-16.76	11.8	Island Fox	Late Holocene	Anacapa

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